

Review of the millipede genus *Plusioglyphiulus* Silvestri, 1923, with descriptions of new species from Southeast Asia (Diplopoda, Spirostreptida, Cambalopsidae)

Sergei I. GOLOVATCH

Institute for Problems of Ecology and Evolution, Russian Academy of Sciences,
Leninsky pr. 33, Moscow 119071 (Russia)
sgol@orc.ru

Jean-Jacques GEOFFROY

Muséum national d'Histoire naturelle,
Département Écologie et Gestion de la Biodiversité,
UMR 7179 du CNRS équipe EVOLTRAIT,
4 avenue du Petit Château, F-91800 Brunoy (France)
geoffroy@mnhn.fr

Jean-Paul MAURIÈS

Muséum national d'Histoire naturelle, Département Systématique et Évolution,
case postale 53, 57 rue Cuvier, F-75231 Paris cedex 05 (France)
collmill@mnhn.fr

Didier VAN DEN SPIEGEL

Musée Royal de l'Afrique centrale,
Leuvensesteenweg 13, B-3080 Tervuren (Belgium)
didier.van.den.spiegel@africamuseum.be

Golovatch S. I., Geoffroy J.-J., Mauriès J.-P. & Van den Spiegel D. 2009. — Review of the millipede genus *Plusioglyphiulus* Silvestri, 1923, with descriptions of new species from Southeast Asia (Diplopoda, Spirostreptida, Cambalopsidae). *Zoosystema* 31 (1): 71-116.

ABSTRACT

The small, basically Southeast Asian genus *Plusioglyphiulus* Silvestri, 1923 is redefined to incorporate, in addition to the five hitherto described species, nine new members: *P. ampullifer* n. sp. from Vietnam, *P. deharvengi* n. sp., *P. foveatus* n. sp. and *P. steineri* n. sp. from Laos, *P. bessonni* n. sp. from Thailand, *P. bedosae* n. sp., *P. pallidior* n. sp. and *P. similis* n. sp. from Kalimantan (Borneo, Indonesia), and *P. hoffmani* n. sp. from Sarawak (Borneo, Malaysia). All of the cavernicolous congeners are presumed to be only troglophiles. A key is provided to all 14 currently known species of the genus.

KEY WORDS

Diplopoda,
Cambalopsidae,
Plusioglyphiulus,
subterranean biology,
cave,
Southeast Asia,
new species.

RÉSUMÉ

Révision des diplopodes du genre Plusioglyphiulus Silvestri, 1923 et description de nouvelles espèces d'Asie du Sud-Est (Diplopoda, Spirostreptida, Cambalopsidae).

Le genre *Plusioglyphiulus* Silvestri, 1923, fondamentalement réparti en Asie du Sud-Est, est redéfini afin d'incorporer, en plus des cinq espèces déjà connues, neuf nouveaux membres : *P. ampullifer* n. sp. du Vietnam, *P. deharvengi* n. sp., *P. foveatus* n. sp. et *P. steineri* n. sp. du Laos, *P. bessoni* n. sp. de Thaïlande, *P. bedosae* n. sp., *P. pallidior* n. sp. et *P. similis* n. sp. du Kalimantan (Bornéo, Indonésie), et *P. hoffmani* n. sp. du Sarawak (Bornéo, Malaisie). Tous les congénères décrits ici sont cavernicoles mais sont supposés troglophiles. Une clé d'identification est donnée pour l'ensemble des 14 espèces maintenant connues de ce genre.

MOTS CLÉS

Diplopoda,
Cambalopsidae,
Plusioglyphiulus,
biologie souterraine,
grotte,
Asie du Sud-Est,
nouvelles espèces.

INTRODUCTION

The rather small, predominantly Southeast Asian genus *Plusioglyphiulus* Silvestri, 1923 was first proposed as a subgenus of *Glyphiulus* Gervais, 1847, to accommodate an aberrant cavernicolous species, *Glyphiulus cavernicolus* Silvestri, 1923, from Borneo (Silvestri 1923). The subgenus was diagnosed by the presence of especially numerous carinae on the body segments, coupled with the peculiar conformation of male legs 1 and 2.

Attems (1938), in his classification of *Glyphiulus*, abandoned *Plusioglyphiulus*, but added another species, *G. dubius* Attems, 1938, described from Cambodia, which he noted as being particularly similar to *G. cavernicolus*. Mauriès (1970) elevated *Plusioglyphiulus* to a full genus, to which he also transferred *G. dubius* and described a third congener, *P. boutini* Mauriès, 1970, from Cambodia. Hoffman (1977) and Mauriès (1983) each provided a review of the genus and added two new species, *P. grandicollis* Hoffman, 1977, from Malaya, and *P. macfarlanei* Mauriès, 1983, from Borneo.

Because a recent catalogue of the Cambalidea Bolman, 1893 is available (Jeekel 2004) and is still entirely valid concerning *Plusioglyphiulus* the nomenclatural history of both the genus and of its constituent species can be briefly summarised as below in Systematics.

This genus has long been considered heterogeneous (Hoffman 1977; Mauriès 1983), chiefly because of the great variation observed in the gonopod

structure of the few known constituent species. This is confirmed here by the new material reported below. However, we prefer to retain the genus *Plusioglyphiulus* for the above five species, as well as the nine new taxa described below, emphasizing instead that, at least for the time being, several natural species groups can be delineated.

Below, a description is given of the available new material, followed by a key to all the constituent species of *Plusioglyphiulus*, and brief analyses of their variation and distribution.

ABBREVIATIONS

MNHN	Muséum national d'Histoire naturelle, Paris;
MZB	Museum Zoologicum Bogoriense, Cibinong, Indonesia;
VMNH	Virginia Museum of Natural History, Martinsville;
ZMUC	Zoological Museum, University of Copenhagen;
ZMUM	Zoological Museum, State University of Moscow;
SEM	scanning electron microscopy.

MATERIAL AND METHODS

The material serving as the basis for the present contribution derives from the subterranean collections made in Vietnam, Laos and Indonesia by Anne Bedos and Louis Deharveng (MNHN), in Kalimantan, Indonesia by Yayuk Suhardjono and Cahyo Rahmadi (MZB), as well as from material taken in Laos (epigeal) and

Thailand (subterranean) by J.-P. Besson. Besides this, Richard L. Hoffman (VMNH) provided several cavernicolous samples from Laos and Malaysia. The bulk of the material has been deposited in MNHN, MZB and VMNH, with a few voucher specimens shared with the collections of ZMUM and ZMUC.

SEM micrographs were taken using a JEOL JSM-6480LV scanning electron microscope. Dried SEM material was coated with gold and, after study, removed from the stubs and returned to alcohol, all these samples being deposited in MNHN.

The carinotaxy formulae in the descriptions below are those proposed by Hoffman (1977), with modifications. The carinotaxy formula of the collum designates the main, uninterrupted crests by Roman numerals; the nearly complete, only barely interrupted ones are also designated by Roman numerals, those frontally interrupted are marked "(a)", those caudally interrupted are marked "(c)". The strongly interrupted crests (with evident gaps) are designated by Arabic numerals, those frontally interrupted are marked "a", while those caudally interrupted are marked "c". The paramedian and median crests are designated by upper case "P" or "M" and by lower case "p" or "m" when uninterrupted or interrupted, respectively. Intermediate tubercles or short crests are referred to as "(t)" without number, but with their respective row shown by a slash. The caudalmost row of short crests, which is very often regular and separated transversely from the anterior row(s), is shown as "/t" or "/(t)". All this allows not only the number but also the location and shape of the respective crest to be indicated (cf. Hoffman 1977). Slashes indicate the division of crests or tubercles into transverse rows. Due to complete symmetry, only the formula corresponding to the left part of the collum is given (from laterad to mesad). Because variation in the formulae appears to be great, sometimes varying even intraspecifically, no typical arrangement and form of the crests on the collum seems to exist in this genus. However, *Plusioglyphiulus* species are generally characterised by a high number of collar crests and tubercles, of which at least 5 + 5 reach the anterior margin of the tergite. In most of the species, several to all of the crests are subdivided into 2-4 parts, often with 1-3 intercalary tubercles present in the posterior half of the collum (mixostichy, as opposed to isostichy,

according to Hoffman [1977]). In contrast to *Glyphiulus* Gervais, 1847 (Golovatch *et al.* 2007a, b), the crests on the collum are always well developed, never being obliterated or reduced. The sole collar crest pattern that appears to be quite stable (though not without exceptions) can be reduced to pp/t/t+ma/t, the caudalmost row of short crests then being regular and set off by a distinct transverse sulcus from the crests or tubercles lying more anteriorly.

For a better understanding of the above explanations, the necessary designations are put on the respective crests or tubercles of the collum of *P. grandicollis* (Fig. 1B). This species is also chosen for one to be able to compare the more simple formula proposed by Hoffman (1977) and that, more elaborate but more exact, applied here.

The carinotaxy pattern of metaterga first shows the number of crests below the ozoporiferous cone (designated as "I"), followed by that between the left and right "I". Slashes correspond to the division of crests or tubercles into transverse rows. Although the symmetry is also complete, when the formula is short, it is given for both sides of the body. When long, however, it again reflects only the left half of the segment. The typical carinotaxy formula of the midbody metaterga in this genus is as follows: 3(2)/3(2)+I/i+3/3(4)/3+m/m+3/3(4)/3+I/i+3(2)/3(2), which is equivalent to 3(2)/3(2)+I/i+3/3(4)/3+m/m. This differs from the typical formulae of *Glyphiulus* species by an increased number of dorsal tubercles on the midbody metaterga (Golovatch *et al.* 2007a, b).

The body segment counts follow Enghoff *et al.* (1993), with minor modifications after Golovatch *et al.* (2007a, b).

SYSTEMATICS

Order SPIROSTREPTIDA Brandt, 1833

Suborder CAMBALIDEA Cook, 1895

Family CAMBALOPSIDAE Cook, 1895

Subfamily GLYPHIULINAE Chamberlin, 1922

Genus *Plusioglyphiulus* Silvestri, 1923

TYPE SPECIES. — *Glyphiulus cavernicolus* Silvestri, 1923, by monotypy [type locality: Bidi Caves, Sarawak, Borneo].

DIAGNOSIS. — 1. Male legs 1 generally strongly reduced, but remaining parts enlarged; sternite with a single, high, median process, strongly unciform in adults, directed frontally and usually supplied with several strong setae at the base on frontal face; coxites usually subconical and setose; telopodites completely reduced, only rarely visible as a minute knob distomedially. This is one of the basic autapomorphies of the genus.

2. Male legs 2 usually strongly enlarged, flattened sagittally, densely hairy on caudal face; tarsus stout, shortened; penes slender, subconical, devoid of setae. This is another strong autapomorphy of the genus.

3. Male legs 3 usually with elongated coxae, but with shortened and compact telopodites. This is a weaker autapomorphy of the genus, since certain species in some other genera of Cambalopsidae show similar conditions.

4. Both collum and segment 2 often very strongly enlarged, as wide as segments of posterior third of body or nearly so, thus making postcollar constriction remarkably narrow. This is a strong autapomorphy of the genus.

5. Pleural regions of segments 2–4 conspicuously expanded ventrad. This is a weak autapomorphy, because several species from other genera of Cambalopsidae show similar conditions.

6. Ventral extensions of male segment 7 especially prominent, usually with ends turned abruptly caudad. This is a weak autapomorphy, because several species from other genera of Cambalopsidae show similar conditions.

7. Carinotaxy patterns of collum highly variable. Crests proper virtually never obliterated or reduced, very often subdivided into 2–4 parts, often with 1–3 intercalary tubercles or short crests; usually 10 crests reaching anterior margin. This is a strong autapomorphy of the genus.

8. The typical carinotaxy pattern of the metaterga is $3/3+I/i+3/3(4)/3+m/(m)/m+3/3(4)/3+I/i+3/3$, thus reflecting the fact that all or most of the dorsal crests or tubercles are arranged in three transverse rows (except *P. bedosae* n. sp. and *P. pallidior* n. sp.). The middle transverse row in adults is sometimes not in line with the two other rows, being intercalary; this row seems to only be attained at or towards the onset of adulthood. The median crest is usually lower than others, never doubled anteriorly. This is a relatively weak autapomorphy, because some species from other genera (e.g., *Glyphiulus bedosae* Golovatch, Geoffroy, Mauriès & Van den Spiegel, 2007) also show three transverse rows of tubercles on the metaterga, whereas two rows seem to regularly occur in immature stadia of some *Plusioglyphiulus* species.

9. The anterior gonopods usually have a plate-like sternum or coxosternum, normally without a median outgrowth; coxites separate or contiguous medially, but never fused, each with one or two distinct processes; telopodites moveable, elongate, subcylindrical, lateral to caudolateral in position, 1-segmented, often curved and setose. This is a rather strong, but not absolute autapomorphy of the

genus, because in many Cambalopsidae representing various genera the anterior gonopods look alike.

10. Posterior gonopods smaller than anterior ones, but usually elongated, not compressed; coxite normally showing an arm or its traces, a shelf-like structure on frontal face and a fovea subapically, devoid of the often plumose flagella that are so characteristic of *Glyphiulus* species. This seems to be a weak autapomorphy, since the variation range in posterior gonopod conformation in *Plusioglyphiulus* is unusually wide.

11. Clypeus with three teeth anteromedially, only seldom variable (*P. pallidior* n. sp.). This is a typical condition occurring throughout Juliformia.

12. Promentum always well separated from eumentum.

SPECIES INCLUDED. — Below is a checklist of the species hitherto assigned to *Plusioglyphiulus*, arranged in alphabetical order (after Jeekel 2004).

1. *Plusioglyphiulus boutini* Mauriès, 1970, described from near Kampong Trach, 10.554°N, 104.471°E, Kampot Province, Cambodia; still known only from the original description (Mauriès 1970), incorporated in later reviews and the most recent key (Hoffman 1977; Mauriès 1983). Listed as a cave-dweller from Cambodia (Boutin 2001).

2. *Plusioglyphiulus cavernicolus* (Silvestri, 1923), type species, described as *Glyphiulus (Plusioglyphiulus) cavernicolus*, from “Bidi Caves” (Silvestri 1923), most probably neither in India nor in Ceylon (*contra* Attems 1936; Mauriès 1970; Jeekel 1971), but near Bau, Sarawak, Borneo (Hoffman 1977), which is at 01.333°N, 110.167°E. This species, which is still known only from the original description (Silvestri 1923), was referred to *Plusioglyphiulus* by Mauriès (1970), and incorporated in later reviews and the most recent key (Hoffman 1977; Mauriès 1983). Koilraj *et al.* (2000) studied the locomotor activity of a population claimed to represent *Glyphiulus cavernicolus* in a cave in the Samanar hill complex (09°58'N, 78°10'E), about 8 km southeast of the Madurai Kamaraj University campus, Madurai, India. However, the identity of their material is highly questionable.

Likewise, the recent records of *P. cavernicolus* in several other caves of Sarawak (Decu *et al.* 2001) are also likely to be misleading (see below).

3. *Plusioglyphiulus dubius* (Attems, 1938), described as *Glyphiulus dubius*, from a single female collected at Angkor, 13.369°N, 103.863°E, Cambodia. Still known only from the original description (Attems 1938). Transferred with doubts to *Plusioglyphiulus* by Mauriès (1970), incorporated in later reviews and in the latest key (Hoffman 1977; Mauriès 1983).

4. *Plusioglyphiulus grandicollis* Hoffman, 1977, described from Batu Caves, 03.171°N, 101.703°E, Kuala Lumpur, Selangor State, Malaysia; still known only from the original description, incorporated in the latest review and key (Hoffman 1977; Mauriès 1983). Listed as a cave-dweller

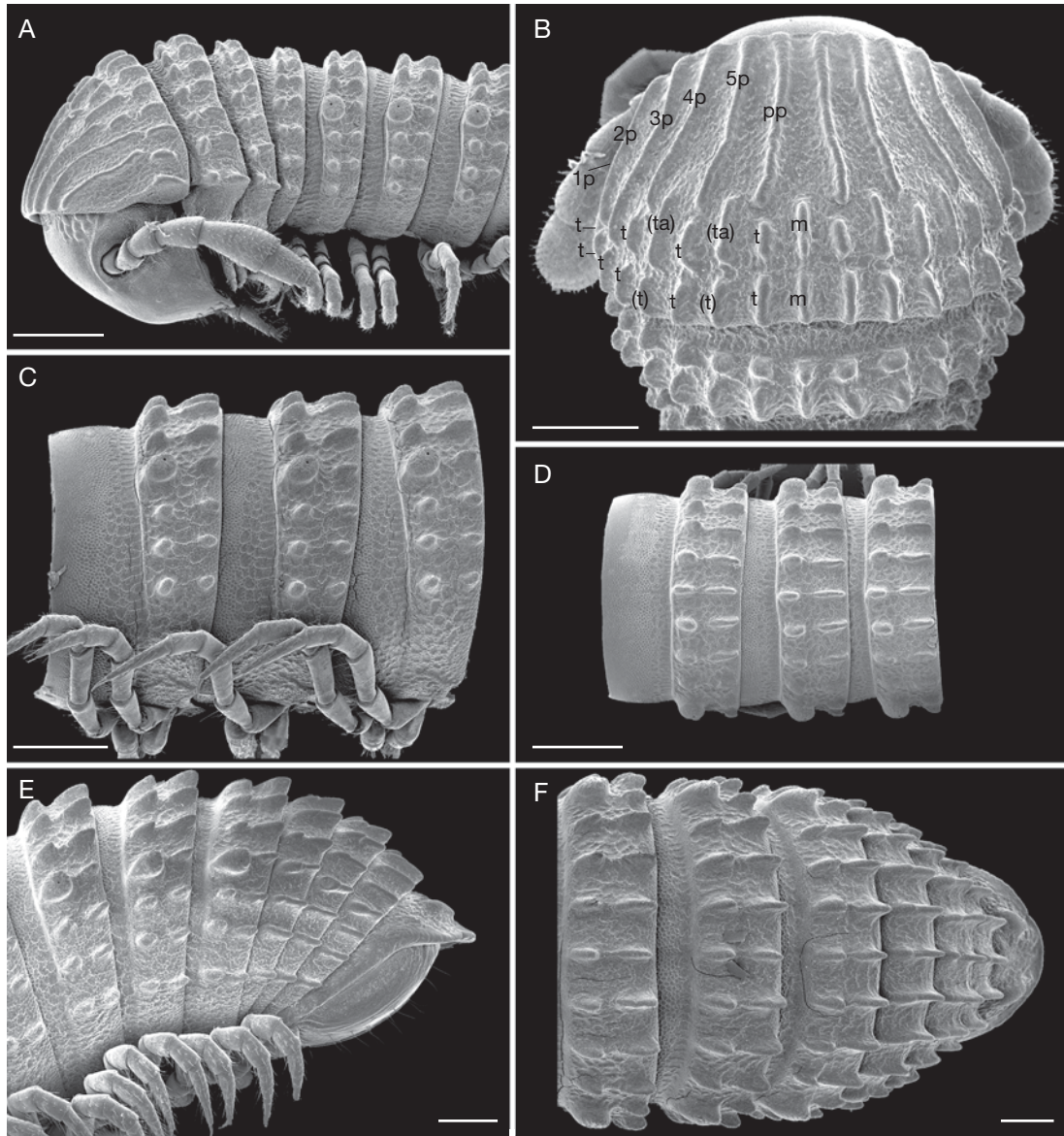


FIG. 1. — *Plusioglyphiulus grandicollis* Hoffman, 1977, near-topotype ♀: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, midbody segments, lateral view; **D**, same, dorsal view; **E**, posterior part of body, lateral view; **F**, same, dorsal view. See text for abbreviations significance. Scale bars: A-D, 0.5 mm; E, F, 0.2 mm.

from Malaysia (Decu *et al.* 2001). This species will be redescribed below based on new material.

5. *Plusioglyphiulus macfarlanei* Mauriès, 1983, described from an unknown locality in Sabah, Borneo, Malaysia; still known only from the original description (Mauriès 1983).

Plusioglyphiulus grandicollis Hoffman, 1977
(Figs 1-3)

Plusioglyphiulus grandicollis Hoffman, 1977: 715. — Mauriès 1983: 272. — Jeekel 2004: 57.

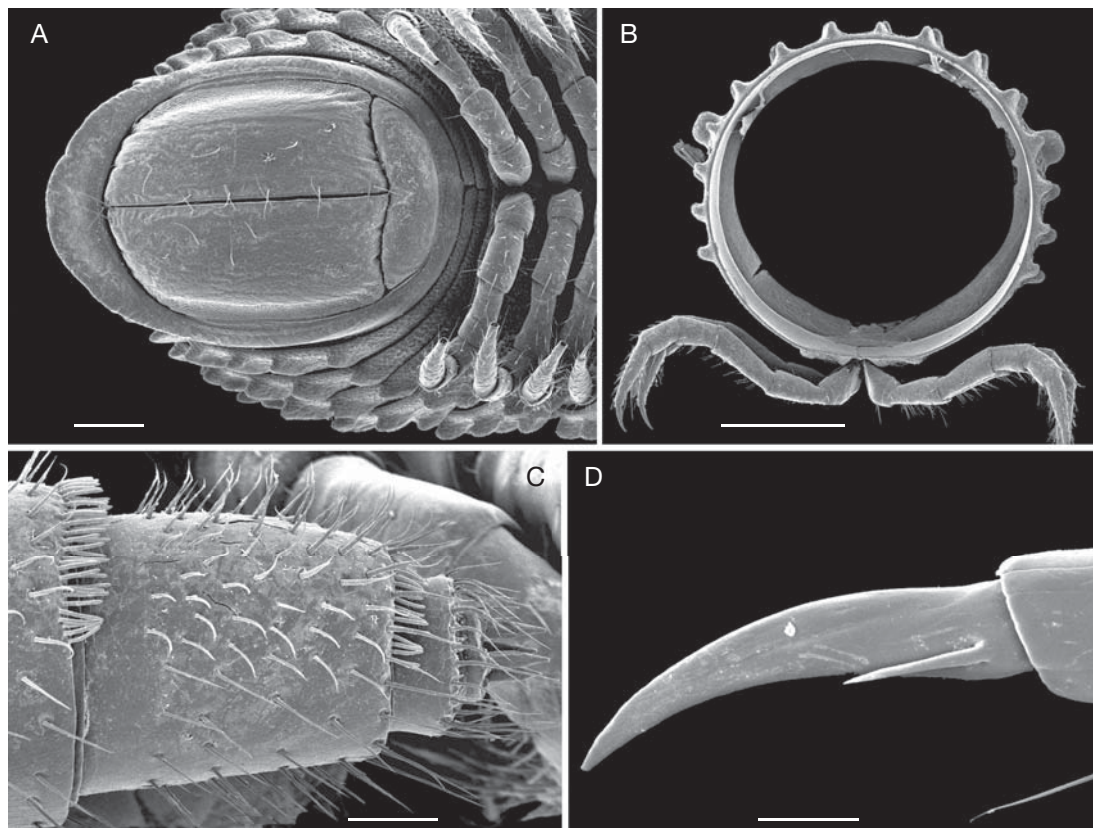


FIG. 2. — *Plusioglyphiulus grandicollis* Hoffman, 1977, near-topotype ♀: **A**, telson, ventral view; **B**, midbody segment section; **C**, sensilla on antennomeres 5 and 6, lateral view; **D**, claw of midbody leg, caudal view. Scale bars: A, 0.2 mm; B, 0.5 mm; C, 0.05 mm; D, 0.02 mm.

NEW MATERIAL. — **Malaysia.** Selangor State, Kuala Lumpur, Batu Cave massif, 03.171°N, 101.703°E, Cave Gua Pandan, 28.I.2001, leg. H. Steiner, 1 ♂, 1 ♀ (VMNH); 1 ♀ (SEM, MNHN GA012).

REDESCRIPTION

Male about 32 mm long and 1.5 mm wide, with 58p+3a+T, collum being broadest; females about 35 and 38 mm long, 1.6 and 1.9 mm wide, with 63p+3a+T and 78p+2a+T, respectively, segments of posterior third of body being broadest. Coloration, including that of collum and segment 2, uniformly grey-brown to brown, dorsal crests and ozoporiferous tubercles usually dark brown.

Surface smooth and polished on frons, very delicately shagreened above. Antennae short and clavate (Fig. 3A), antennomeres 6 and 7 each with a large

group of bacilliform sensilla distodorsally (Fig. 2C). Ocellaria transversely subreniform, with 9–12 blackish ocelli in 5 or 6 longitudinal rows, but without adjacent darker spots dorsally. Gnathochilarium oligotrichous, each lamella lingualis with 3 or 4 setae.

Postcollar constriction very evident, due to especially enlarged collum and segment 2 (Fig. 1B). Carinotaxy formula of collum: 1p/t+2p/t+3p/t+(ta)/(t)+4p/t/t+(ta)/(t)+5p/t/t+(ta)/(t)+pp/t/t+ma/t (Fig. 1A, B). Carinotaxy of metatergum 2, 7/7+m/m+7/7; of metaterga 3 and 4, 7/7+M(m/m)+7/7; of metatergum 5 and subsequent metaterga, except last few, 3/3+I/i+3/3+m/m+3/3+I/i+3/3; of apodous segments, usually 7+m+7 (Fig. 1); all crests and tubercles, including poriferous cones, rather low; poriferous tubercles (I) only slightly higher, broader

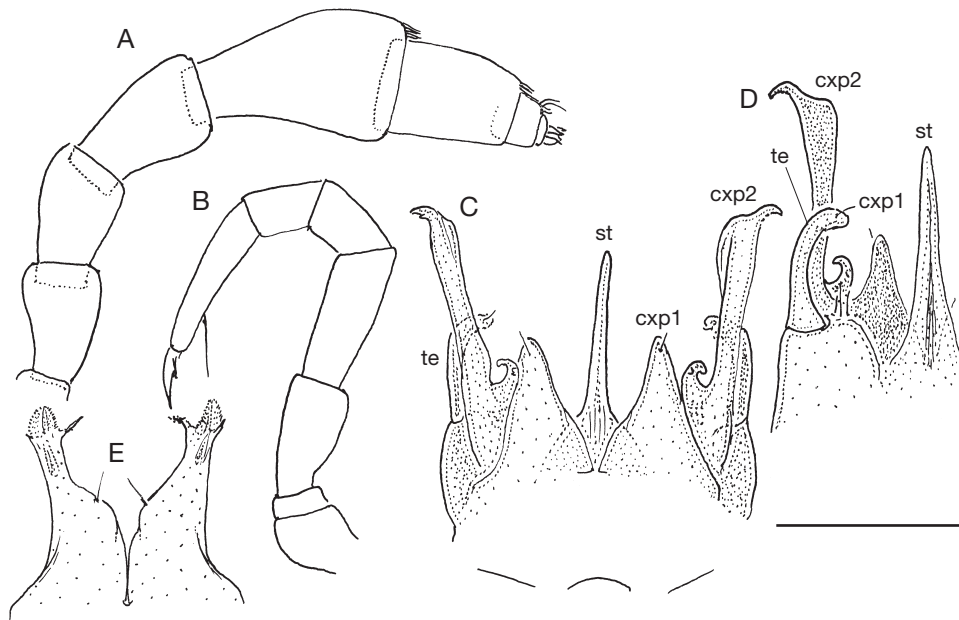


FIG. 3. — *Plusioglyphiulus grandicollis* Hoffman, 1977, near-topotype ♂: **A**, antenna, lateral view; **B**, midbody leg; **C**, anterior gonopods, frontal view; **D**, same, caudal view; **E**, posterior gonopods, frontal view. Abbreviations: **cxp**, coxal process; **st**, sternal process; **te**, telopodite. Scale bar: 0.3 mm.

than high, but median ones (m) slightly lower than others (Figs 1C, D; 2B). Dorsal crests on several posteriormost segments considerably higher than others (Fig. 1E). Midbody segments circular in cross-section (Fig. 2B). Pleural regions of segments 2–4 conspicuously expanded, flap-shaped, especially so on segment 3 (Fig. 1A). An evident, transverse pleural ridge behind gonopod aperture on male segment 7, with rounded flaps bent abruptly caudad. Tegument of metazona delicately alveolate-areolate and dull throughout, stricture between pro- and metazona striolate longitudinally, other parts of prozona very finely shagreened. Metatergal setae absent. Limbus extremely finely and more or less regularly denticulate. Epiproct broadly rounded and cariniform apically, with 2+m+2 tubercles dorsally at midway, of which the lateralmost and, especially, the median can be very low; paraprocts regularly convex, devoid of an elevation at midline; hypoproct emarginate at caudal margin (Fig. 2A).

Legs rather short, about 2/3 as long as body diameter (Fig. 2B), claws with an evident spine near base

(Figs 2D; 3B). Tarsi very delicately fringed apically; most of distal setae with scattered denticles.

Male legs 1 with elongate, conical, setose coxites and a single, very large, falcate, median sternal process with several long setae at base on frontal face. Male legs 2 evidently enlarged, coxae deeply emarginate distally on caudal face, telopodite densely hirsute on frontal face; penes conical, elongated, bare, fused at base. Male legs 3 with particularly elongate and slender coxae, but with compact telopodites.

Anterior gonopods (Fig. 3C, D) with a long, slender, median sternal process (st); coxite with a paramedian pair of low inner processes (cxp1) and another pair of long, slender, outer, distally beak-shaped processes (cxp2) with a short uncus at base; telopodites (te) slender, curved, attached to coxal region caudolaterally, capable of movement, almost non-setose even subapically. Posterior gonopods small, rather simple, coxites well separated from sternum, at least on caudal face (Fig. 3E), each with a spiniform structure medio-subapically and a complex fringed apex.

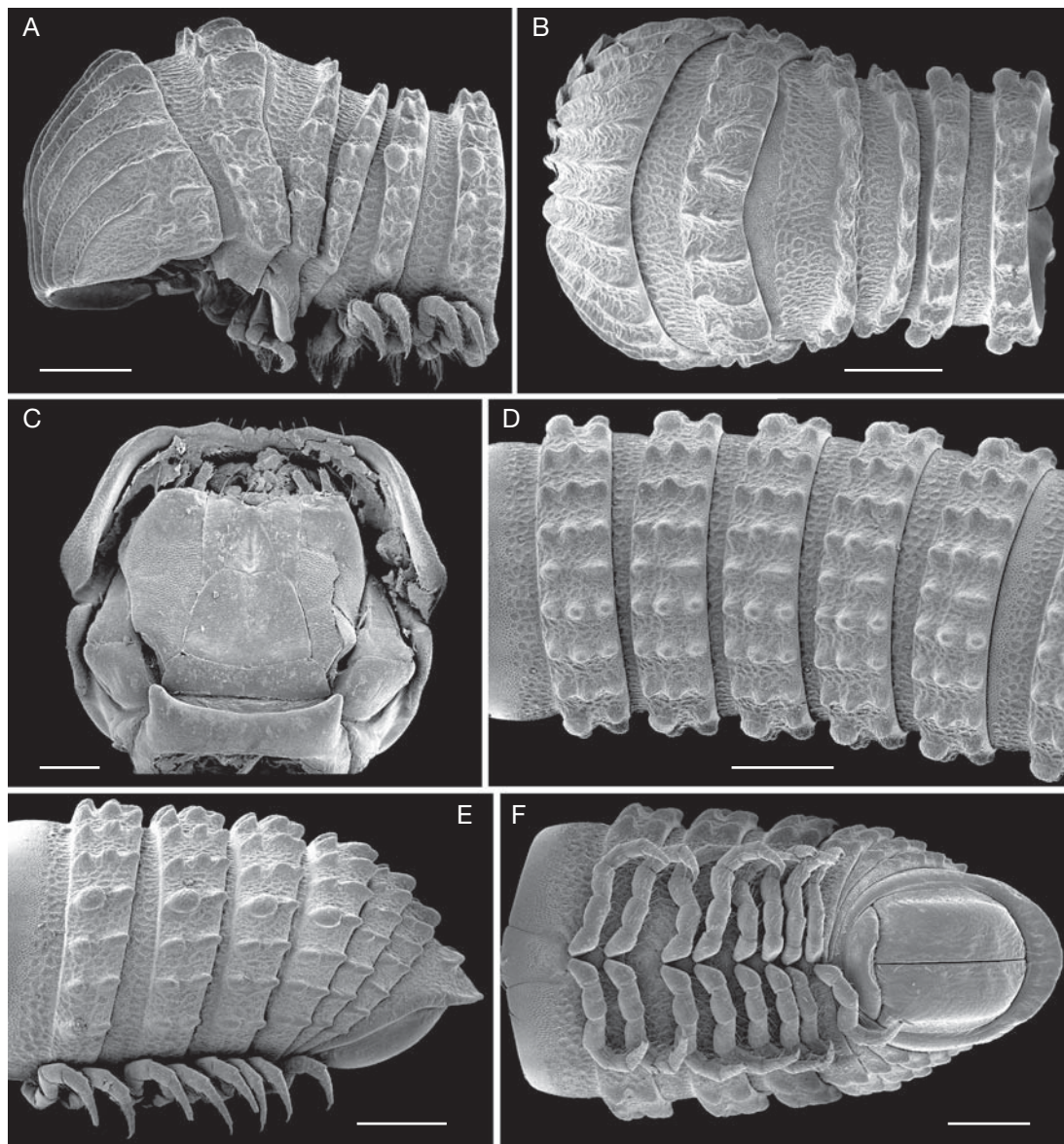


FIG. 4. — *Plusioglyphiulus ampullifer* n. sp., paratype ♂: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, gnathochilarium, ventral view; **D**, midbody segments, dorsal view; **E**, posterior part of body, lateral view; **F**, same, ventral view. Scale bars: A, B, D-F, 0.5 mm; C, 0.2 mm.

REMARKS

Hoffman (1977) described this species from Batu Caves, so the above material can be considered as near-topotypic. It agrees well with the original description, but differs slightly in showing only

7/7+m/m+7/7, not 8/8+m/m+8/8, tubercles on segments 2-4, sometimes a lower number of dorsal tubercles (4 or 5, not 7) on the epiproct, and the presence on the legs of a strong spine at the base of the claw.

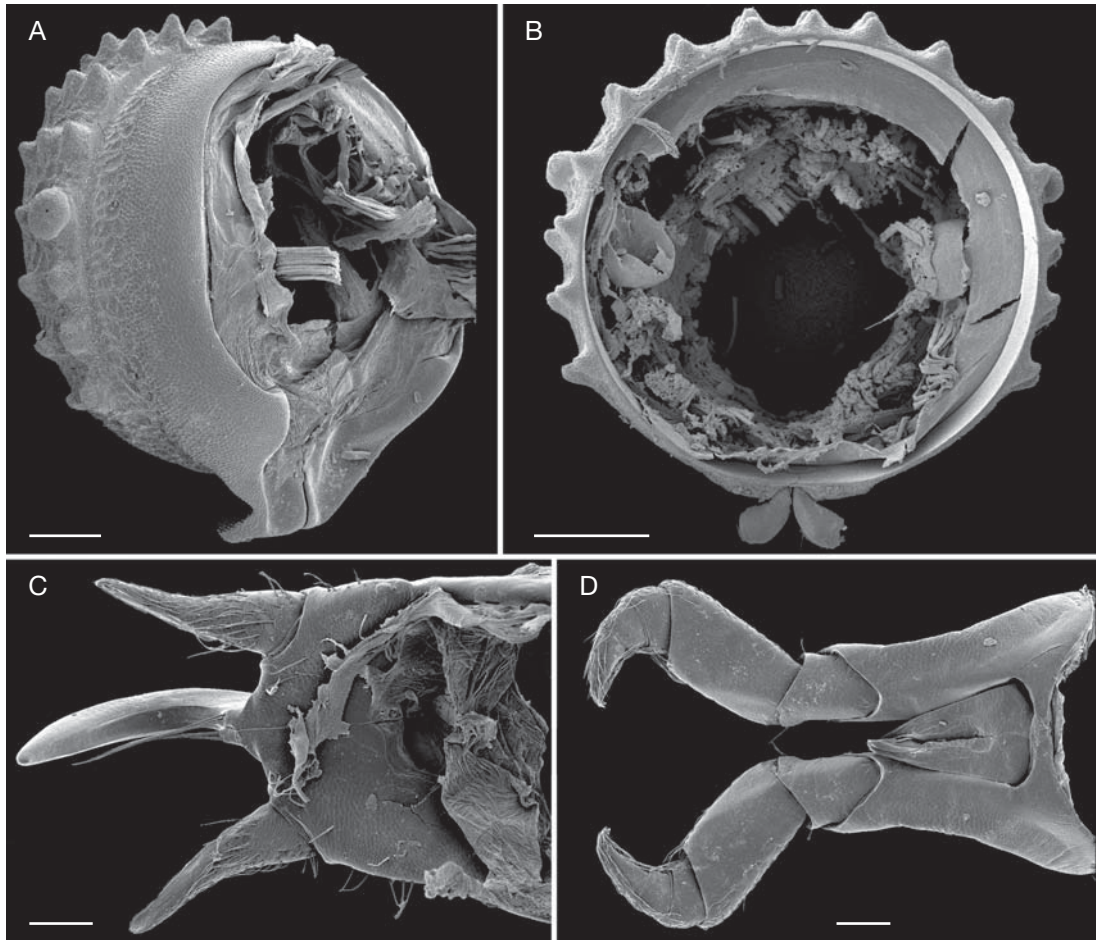


FIG. 5. — *Plusioglyphiulus ampullifer* n. sp., paratype ♂: **A**, segment 7, frontolateral view; **B**, midbody segment section; **C**, leg 1, frontal view; **D**, leg 2, frontal view. Scale bars: A, 0.2 mm; B, 0.5 mm; C, D, 0.1 mm.

Any obvious troglomorphic traits in this species seem to be absent.

Plusioglyphiulus ampullifer n. sp.
(Figs 4-7)

TYPE MATERIAL. — **Vietnam**. Dong Nai Prov., Dinh Quan, 11.27°N, 107.22°E, lava tube 1, 23.XII.1994, leg. L. Deharveng, Truong Quang Tam & A. Bedos (VIET-048), holotype ♂ (MNHN GA055); 1 ♂ paratype (MNHN GA055); 1 ♂ paratype (SEM); 1 ♂ paratype (ZMUM).

ETYMOLOGY. — To emphasize the ampulliform distal part of the posterior gonopods.

DIAGNOSIS. — Differs from congeners by certain details of gonopod structure (very characteristic shapes of the various outgrowths and processes), coupled with the isostichic carinotaxy of the collum and of other body segments, the flattened paraprocts, the broadly rounded epiproct and the presence of spots dorsad of the ocellaria.

DESCRIPTION

Length 30-35 mm, width 2.0-2.2 mm, collum being broadest. Coloration mainly dirty brown to red-brown, only collum and, in part, head and segment 2 contrastingly yellowish; metatergal crests/tubercles usually dark brown to blackish, due to heavy sclerotization; ocellaria black, head dorsad

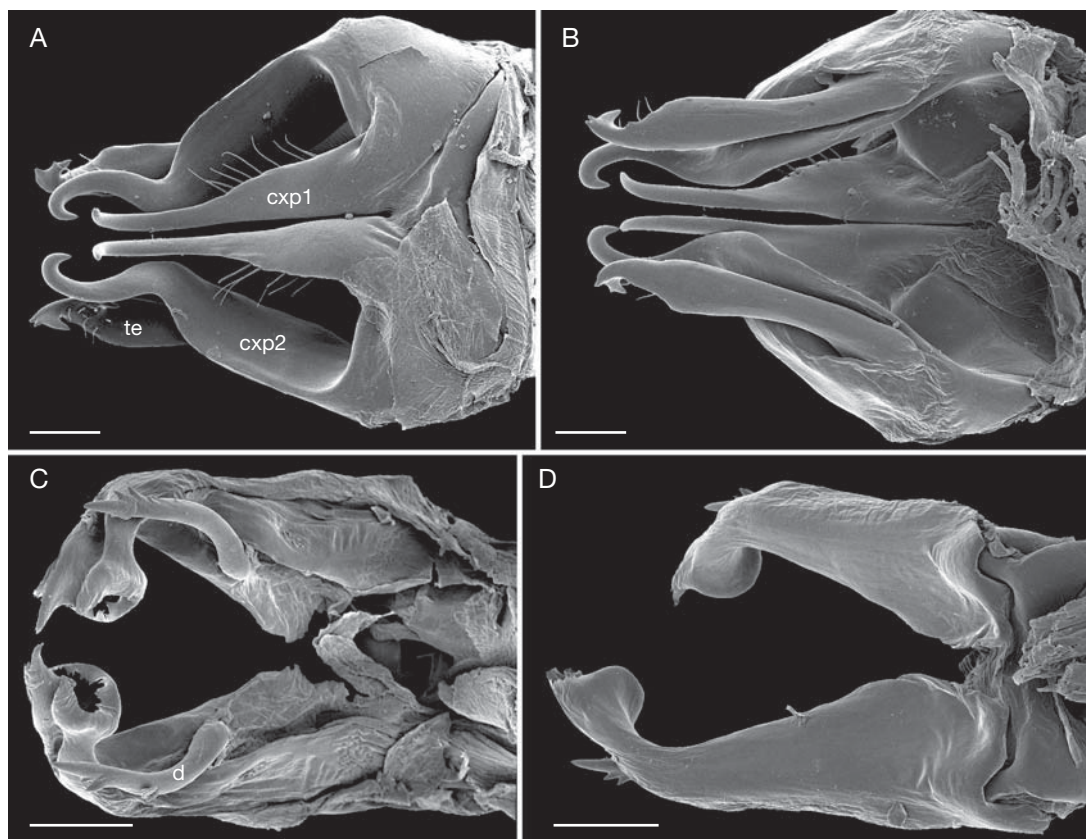


FIG. 6. — *Plusioglyphiulus ampullifer* n. sp., paratype ♂: **A**, anterior gonopods, frontal view; **B**, same, caudal view; **C**, posterior gonopods, frontal view; **D**, same, caudal view. Abbreviations: **cxp**, coxal process; **d**, flagelliform arm; **te**, telopodite. Scale bars: 0.1 mm.

of ocellaria with 1+1, nearly contiguous, marbled brown spots; antennomeres 5 (distally) to 7 (entirely) usually dark brown; both a narrow axial line and a broader stripe level to ozopores grey-brown, usually distinct; legs and venter yellow-brown, only distal podomeres slightly reddish.

Body with 55-72p+2a+T. Length of holotype about 30 mm, width 2.0 mm, with 58p+2a+T.

Antennae relatively short and clavate (Fig. 7A), antennomeres 6 and 7 each with a small group of bacilliform sensilla distodorsally (Fig. 7A). Ocellaria black, ovoid in shape, with 18-20 ocelli in 5 or 6 longitudinal rows. Gnathochilarium (Fig. 4C) oligotrichous.

Postcollar constriction very evident, due to especially enlarged collum and segment 2 (Fig. 4B).

Carinotaxy formula of collum: I+t/t+3p/t+IV+V(a)+VI+7a+P+ma (Fig. 4A, B). Carinotaxy of metatergum 2, 7/7+m/m+7/7, anterior parts of all crests except "m" transverse, those of "m" longitudinal; formula of metaterga 3 and 4, 4/4+3+m+3+4/4, of which 3+m+3 rounded and placed transversely; formula of metatergum 5, 3/3+I/i+3/3+m+3/3+I/i+3/3; formula of subsequent metaterga, except last few, 3/3+3+I/i+3/3+m/m+3/3+3+I/i+3/3; formula of last ozoporiferous metatergum, 3/3+I/i+3/3+m/m+3/3+I/i+3/3; that of apodous segments, 2+5/5+m/m+5/5+2 (Fig. 4A-E); all crests and tubercles, including poriferous cones, rather low. Dorsal crests on several posteriormost segments considerably higher than others (Fig. 4E). Midbody segments circular in cross-section (Fig. 5B). Pleural

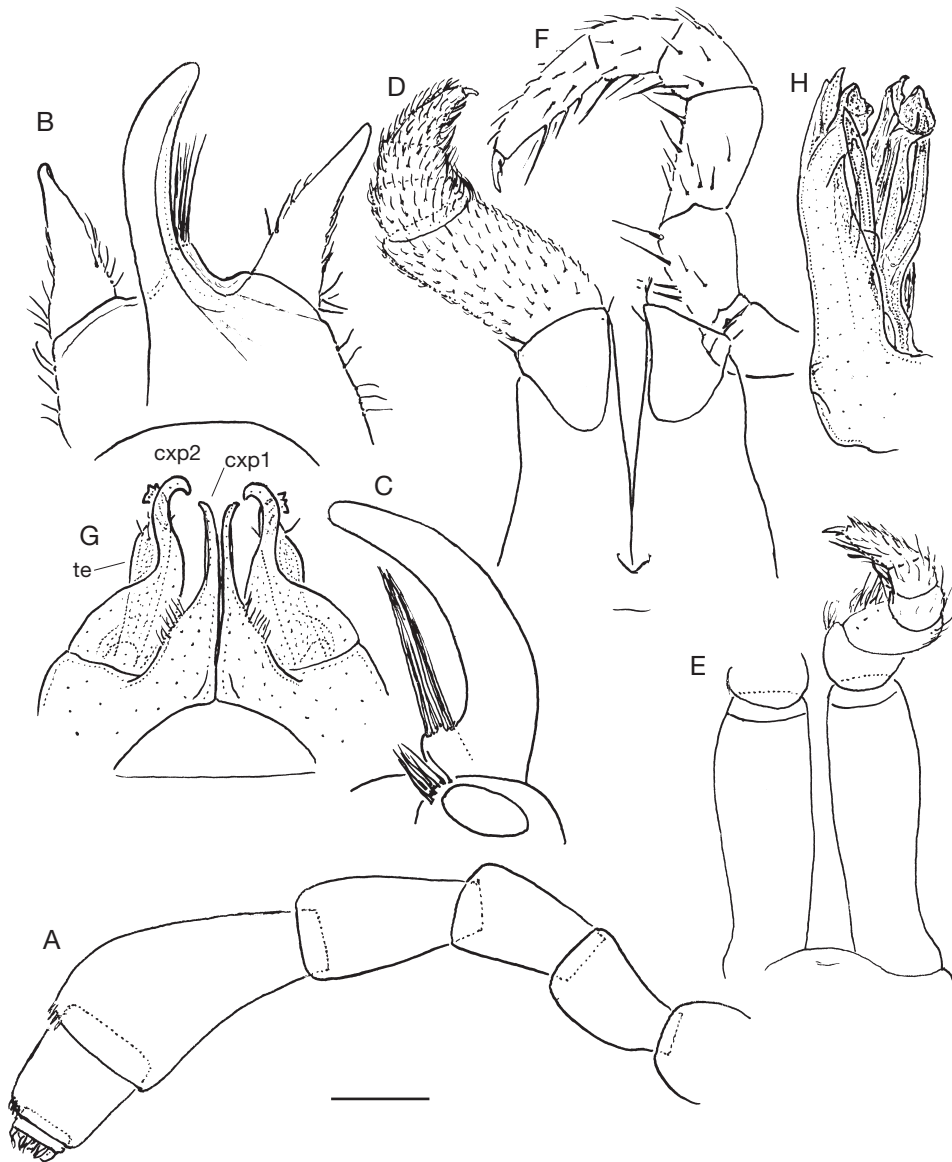


FIG. 7. — *Plusioglyphiulus ampullifer* n. sp., paratype ♂: **A**, antenna, lateral view; **B**, legs 1, subcaudal view; **C**, same, lateral view; **D**, leg 2, caudal view; **E**, legs 3, caudal view; **F**, leg 6; **G**, anterior gonopods, frontal view; **H**, posterior gonopods, sublateral view. Abbreviations: **cxp**, coxal process; **te**, telopodite. Scale bar: 0.2 mm.

regions of segments 2–4 conspicuously expanded, flap-shaped, especially so on segment 3 (Fig. 4A). An evident, transverse pleural ridge behind gonopod aperture on male segment 7, with rounded flaps bent abruptly caudad (Fig. 5A). Tegument

and limbus as in *P. grandicollis*. Epiproct broadly rounded apically, with 1+1 paramedian tubercles at midway; paraprocts evidently flattened, without an elevation at midline; hypoproct emarginate at caudal margin (Fig. 4E, F).

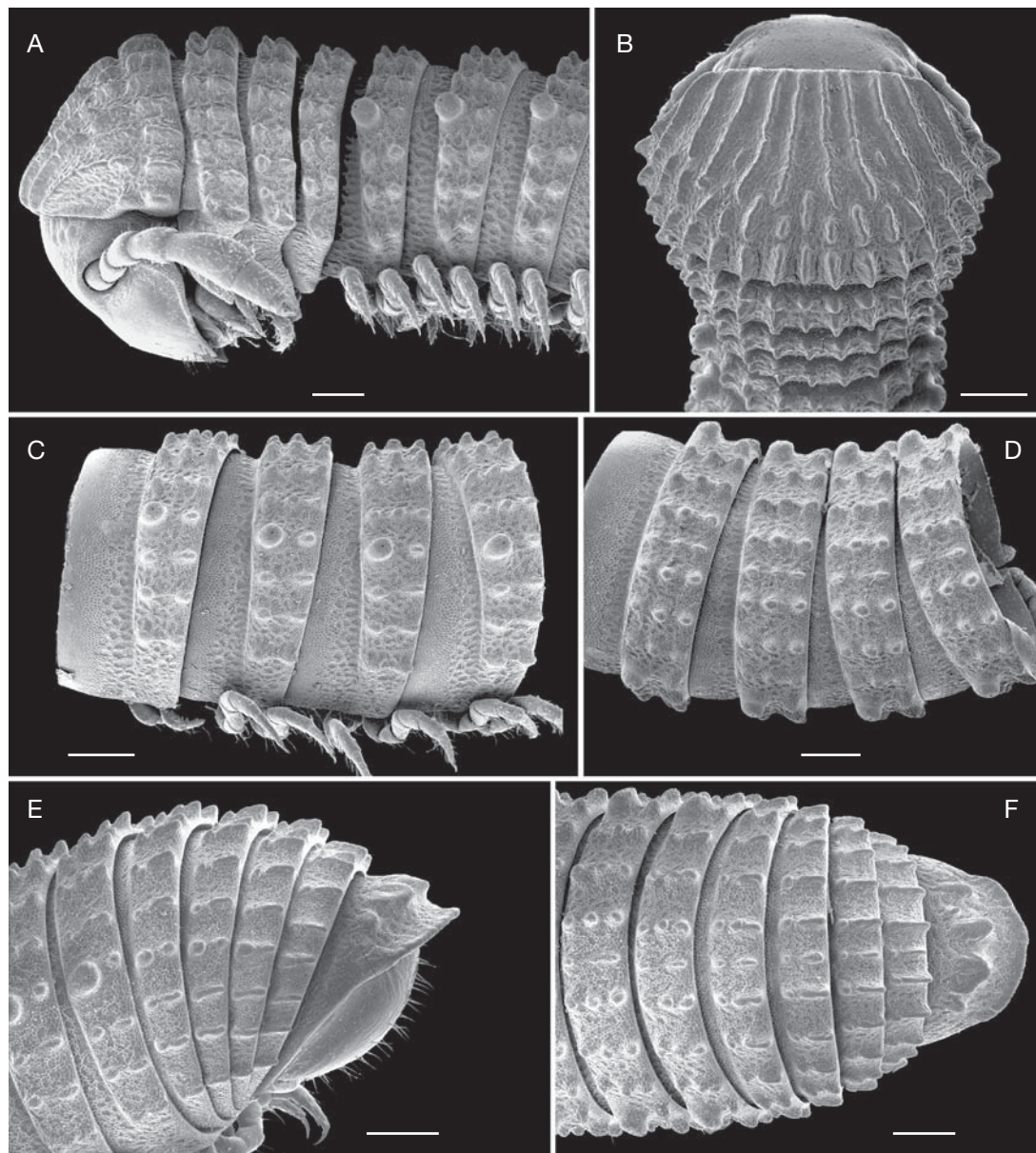


FIG. 8. — *Plusioglyphiulus foveatus* n. sp., paratype ♀: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, midbody segments, lateral view; **D**, same, dorsal view; **E**, caudal part of body, lateral view; **F**, same, dorsal view. Scale bars: 0.2 mm.

Legs short, about half as long as body diameter (Fig. 5B), claws with an evident spine near base (Fig. 7F). Tarsi and tarsal setae as in *P. grandicollis*.

Male legs 1-3 as in *P. grandicollis*. Male legs 1 with elongate, setose coxites and a single, very large, falcate, median sternal process with several long setae at base on frontal face (Figs 5C; 7B, C). Male legs 2

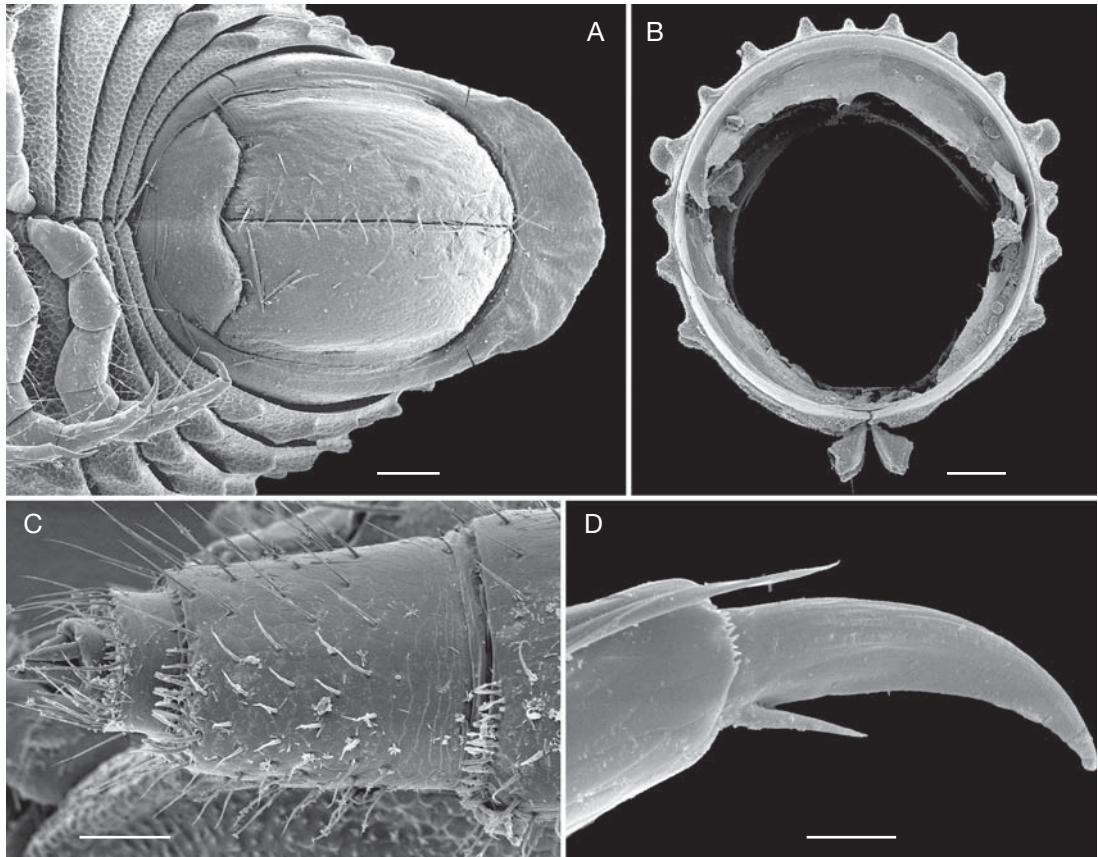


FIG. 9. — *Plusioglyphiulus foveatus* n. sp., paratype ♀: **A**, telson, ventral view; **B**, midbody segment section; **C**, sensilla on antennomeres 5-7, sublateral view; **D**, claw of midbody leg. Scale bars: A, 0.1 mm; B, 0.2 mm; C, 0.05 mm; D, 0.01 mm.

evidently enlarged, telopodite hirsute on frontal face; penes subtriangular, fused at base (Figs 5D; 7D). Male legs 3 with particularly elongate and slender coxae, and shortened telopodites (Fig. 7E).

Anterior gonopods with a paramedian pair of high, slender, apically curved, contiguous but free coxosternal processes (cxp1) anteriorly, each with several lateral setae in basal half; coxal region produced mesad into a slender sigmoid process (cxp2); telopodites (te) elongate, attached to coxal region on caudal face, probably capable of movement, carrying a few setae subapically and tridentate apically (Figs 6A, B; 7G). Posterior gonopods small, complex, coxites well separated from sternum, at least on caudal face (Figs 6C, D; 7H); frontal face of each coxite with a strong, dentate arm (d) at

midway and a complex ampulla-like structure with several teeth nearby.

REMARKS

Any obvious troglomorphic traits in this species seem to be absent.

Plusioglyphiulus foveatus n. sp. (Figs 8-10)

TYPE MATERIAL. — Laos. Luang Prabang Prov., 19.88°N, 102.14°E, W of Tham, 3.VIII.1992, leg. J.-P. Besson, holotype ♂ (MNHN GA056); 1 ♀ paratype (MNHN GA056); 1 ♂ paratype (SEM).

ETYMOLOGY. — To emphasize the foveate apex of the posterior gonopods.

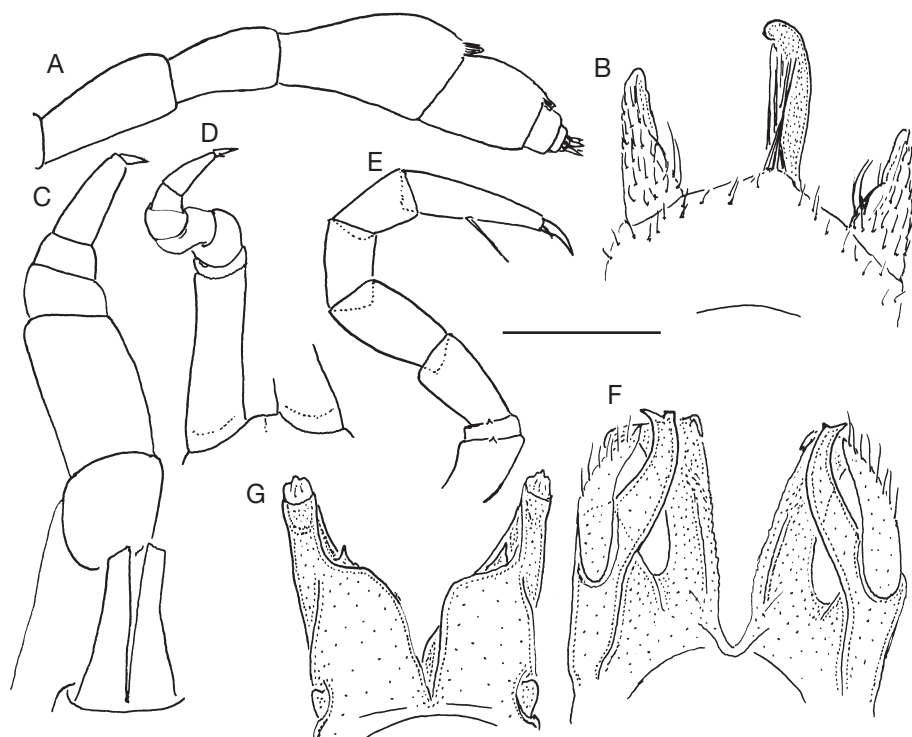


FIG. 10. — *Plusioglyphiulus foveatus* n. sp., paratype ♂: **A**, antenna, lateral view; **B**, legs 1, frontal view; **C**, leg 2, caudal view; **D**, leg 3, caudal view; **E**, midbody leg; **F**, anterior gonopods, caudal view; **G**, posterior gonopods, frontal view. Scale bar: 0.3 mm.

DIAGNOSIS. — Differs from congeners by certain details of gonopod structure (characteristic shapes of the different outgrowths and processes), coupled with the mixostichic carinotaxy of the collum, the isostichic carinotaxy of other body segments, the convex paraprocts, the broadly rounded epiproct and the presence of spots dorsad of the ocellaria.

DESCRIPTION

Length 28–35 mm, width 1.3–1.9 mm, collum and midbody segments being equally broadest.

Coloration whitish to yellow-brown; collum and, partly, head and segment 2 entirely pale; tips of most of tergal crests/tubercles, as well as a narrow axial line and a slightly broader lateral stripe level to ozopores pale grey-brown to brown; ocellaria dark brown with pale to dark brown, widely separated spots dorsally.

Body with 49–66p+4–1a+T. Length of holotype about 30 mm, width 1.3 mm, with 58p+2a+T.

Antennae rather short and clavate (Fig. 10A), antennomeres 6 and 7 each with a considerable

group of bacilliform sensilla distodorsally; similar but minute sensilla present also on antennomere 7 (Fig. 9C). Ocellaria black, ovoid in shape, with 10–13 ocelli in 5–7 longitudinal rows. Gnathochilarium oligotrichous.

Postcollar constriction evident, but collum and segment 2 relatively modestly enlarged (Fig. 8B). Carinotaxy formula of collum: ta/t+2p/t+3p/t+4p/t/t+ta/5/t+(ta)/t+VI(p)/t+pp/t/t+ma/t (Fig. 8A, B). Carinotaxy of metaterga 2–4, 7/7+m/m+7/7, all crests being longitudinal; formula of metaterga 5 to 15, 3/3+I/I+3/3/3+m/m+3/3/3+I/I+3/3/3; formula of subsequent metaterga usually 3/3+I/I+3/3/3+m/(m)/m+3/3/3+I/I+3/3; that of apodous segments, 3+4/4+m/m+4/4+3 (Fig. 8); all crests and tubercles rather high, poriferous cones (I) much higher, nearly as high as broad, but median ones (m) very low (Fig. 9B). Dorsal crests on several posteriormost segments considerably higher than others (Fig. 8E). Midbody segments circular in

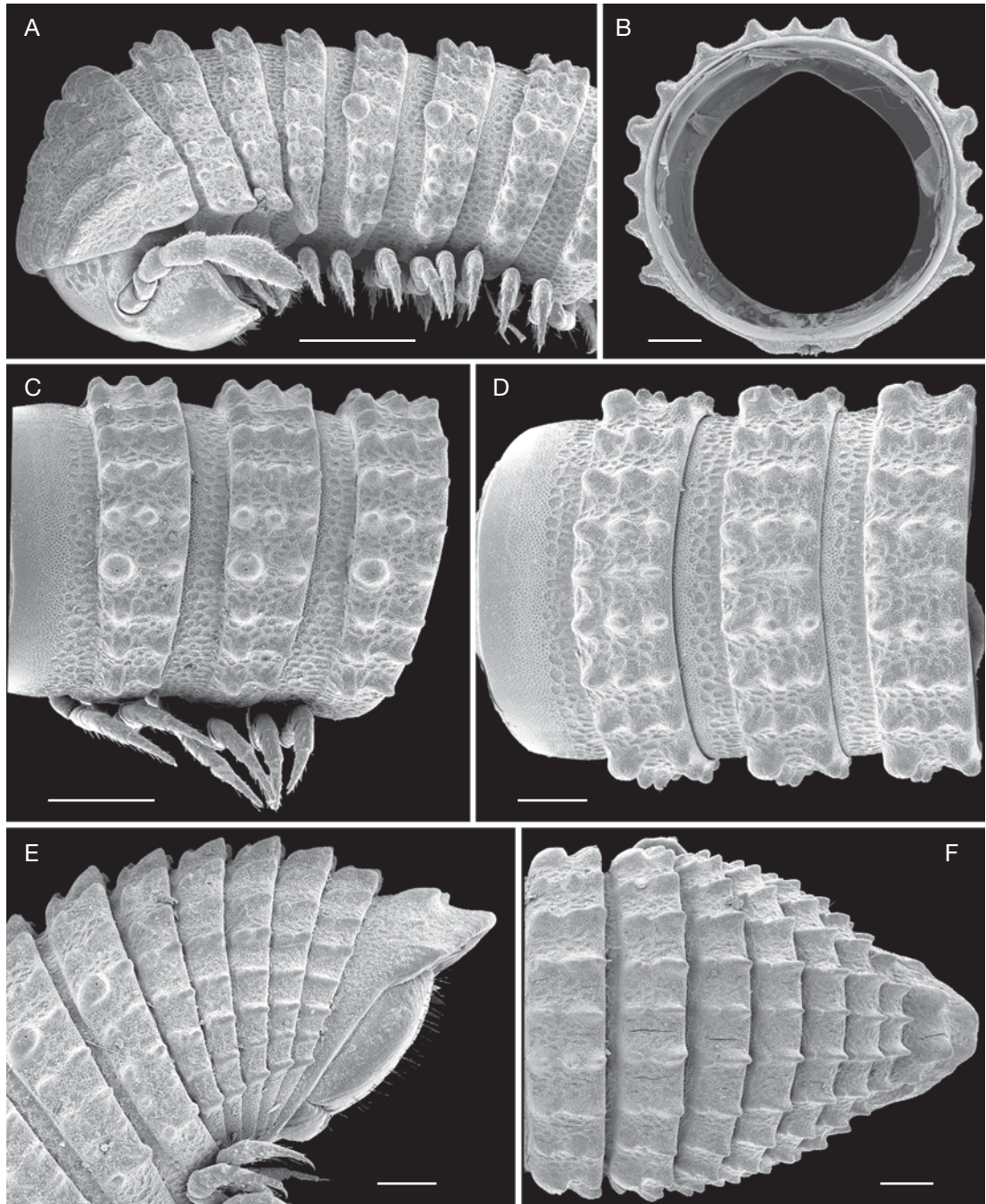


FIG. 11. — *Plusioglyphiulus bessoni* n. sp., paratype ♀: **A**, anterior part of body, lateral view; **B**, midbody segment section; **C**, midbody segments, lateral view; **D**, same, dorsal view; **E**, caudal part of body, lateral view; **F**, same, dorsal view. Scale bars: A, C, 0.5 mm; B, D-F, 0.2 mm.

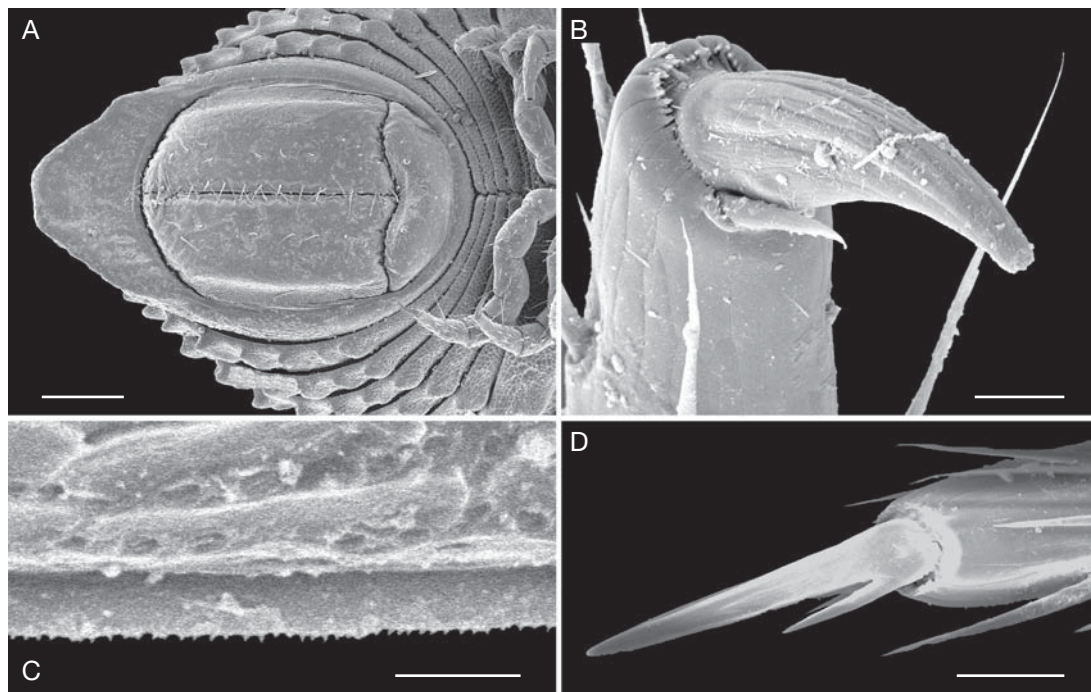


FIG. 12. — *Plusioglyphiulus bessoni* n. sp., paratype ♀: **A**, telson, ventral view; **B**, claw of midbody leg, ventral view; **C**, limbus, dorsal view; **D**, same, subapical view. Scale bars: A, 0.2 mm; B, 0.02 mm; C, 0.005 mm; D, 0.01 mm.

cross-section (Fig. 9B). Pleural regions of segments 2–4 conspicuously expanded, flap-shaped, especially so on segment 3 (Fig. 8A). An evident, transverse pleural ridge behind gonopod aperture on male segment 7, with rounded flaps bent abruptly caudad. Tegument and limbus as in *P. grandicollis* or *P. ampullifer* n. sp. Epiproct broadly rounded and cariniform apically, with 2+2 paramedian tubercles at midway; paraprocts regularly convex, not flattened; hypoproct emarginate at caudal margin (Fig. 9A).

Legs short, on midbody segments about $\frac{2}{3}$ as long as segment diameter (Fig. 9B). Claw at base with a strong accessory spine almost half as long as claw itself (Figs 9D; 10E). Tarsi, tarsal setae and male legs 1–3 (Fig. 10B–D) as in *P. grandicollis*.

Anterior gonopods (Fig. 10F) much like in *P. ampullifer* n. sp., but processes cyp1 large, non-contiguous, flattened sagittally and each carrying a short medial uncus apically; processes cyp2 slightly curved, slender and bifid; telopodites (te) simple,

movable, elongate-subconical, setose laterally in distal half. Posterior gonopods (Fig. 10G) relatively simple, with a pair of strongly reduced telopodites (te) laterally at base; coxite with short denticles (d) instead of arms, fovea-shaped apically.

***Plusioglyphiulus bessoni* n. sp.**
(Figs 11–13)

TYPE MATERIAL. — **Thailand**. Nan, 18.776°N, 100.783°E, Cave Tham Pha Tup (Tham Phra), 10–11.VIII.1992, leg. J.-P. Besson, holotype ♂ (MNHN GA057); 2 ♂♂ paratypes, 1 ♀ paratype (MNHN GA057); 1 ♀ paratype (ZMUM); 1 ♀ paratype (SEM).

ETYMOLOGY. — To honour Jean-Pierre Besson, who collected this material.

DIAGNOSIS. — Differs from congeners by certain details of gonopod structure (complicated anterior gonopods versus strongly simplified posterior ones), coupled with the mixostichic carinotaxy of the collum, the isostichic

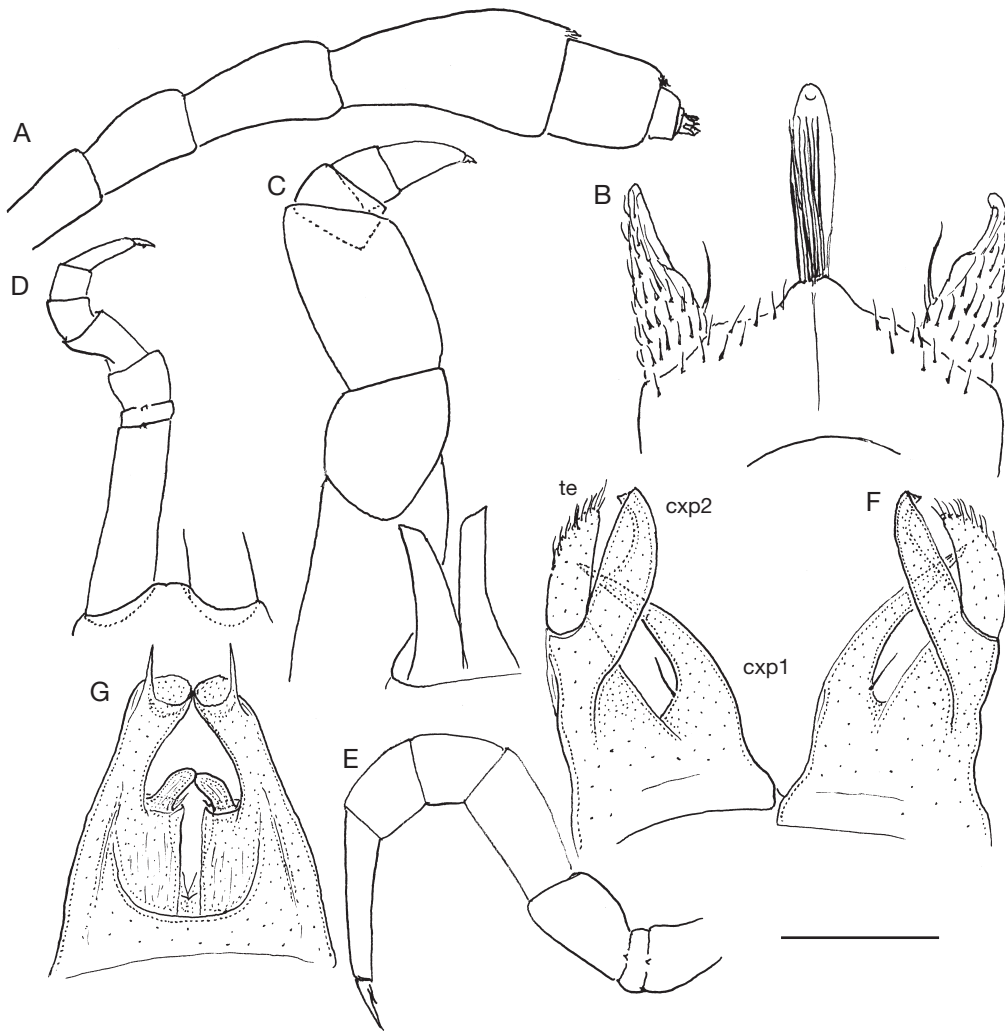


FIG. 13. — *Plusioglyphiulus bessoni* n. sp., paratype ♂: **A**, antenna, lateral view; **B**, leg 1, frontal view; **C**, leg 2, caudal view; **D**, leg 3, caudal view; **E**, midbody leg; **F**, anterior gonopods, frontal view; **G**, posterior gonopods, caudal view. Abbreviations: **cxp**, coxal process; **te**, telopodite. Scale bar: 0.3 mm.

carinotaxy of other body segments, the convex paraprocts, the subtrapeziform epiproct and the absence of spots dorsad of the ocellaria.

DESCRIPTION

Length 25–43 mm, width 1.7–2.0 mm, collum and midbody segments being equally broadest.

Coloration usually uniformly grey-brown, sometimes with a paramedian pair of more or less wide, grey-yellowish stripes; collum and, in part, head

and segment 2 entirely pale; tips of tergal crests/tubercles usually dark brown; ocellaria dark brown to blackish, devoid of adjacent spots dorsally.

Body with 56–75p+4–1a+T. Length of holotype about 34 mm, width 2.0 mm, with 61p+4a+T.

Antennae more elongate (Fig. 13A), antennomeres 6 and 7 each with a small group of bacilliform sensilla distodorsally. Ocellaria transverse and ribbon-shaped, with 10–13 ocelli in 5–7 longitudinal rows. Gnathochilarium oligotrichous.

Postcollar constriction evident, but collum and segment 2 relatively modestly enlarged (Fig. 11A). Carinotaxy formula of collum: $ta/t+2p/t+/(t)+3p/t/t+4p/t/t+(ta)/(t)/(t)+5p/t/t+(ta)/t+pp/t+ma/t$ (Fig. 11A). Carinotaxy of metaterga 2 and 3, $8/8+m/m+8/8$, all crests being longitudinal; formula of metatergum 4, $2+6/6+m/m+6/6+2$; formula of metaterga 5-7, $3/3+I/i+3/3+3+m/m+3/3+I/i+3/3$; formula of subsequent metaterga, $3/3+I/i+3/3+3+m/m+3/3+I/i+3/3$; that of apodous segments, $3(4)+4(3)/4(3)+M(m/m)+4(3)/4(3)+3(4)$ (Fig. 11A, C-F); all crests and tubercles rather high, poriferous cones (I) only slightly higher, and median ones (m) slightly lower, than others (Fig. 11B-E). Dorsal crests on several posterior-most segments considerably higher than others (Fig. 11E). Midbody segments circular in cross-section (Fig. 11B). Pleural regions of segments 2-4 conspicuously expanded, flap-shaped, especially so on segment 3 (Fig. 11A). Pleural ridge behind gonopod aperture on male segment 7, tegument and an extremely finely and more or less regularly denticulate limbus (Fig. 12C) as in other congeners. Epiproct relatively long, produced caudally and broadly subtrapeziform apically, with 1+1 paramedian tubercles at midway; paraprocts regularly convex, not flattened; hypoproct emarginate at caudal margin (Figs 11E; 12A).

Legs short, on midbody segments about half as long as segment diameter (Fig. 13E). Claw at base with a strong accessory spine almost half as long as claw itself (Figs 12B, D; 13E). Tarsi, tarsal setae and male legs 1-3 (Fig. 13B-D) as in *P. grandicollis*.

Anterior gonopods (Fig. 13F) much like in *P. ampullifer* n. sp., but processes $cxp1$ spiniform and non-contiguous; processes $cxp2$ slightly curved, broad, each with a flange on frontal face; telopodites (te) simple, lateral in position, movable, subcylindrical, setose laterally in distal half. Posterior gonopods (Fig. 13G) relatively simple, without traces of telopodites; each coxite with a short sacciform structure (d) instead of arms, fovea-shaped apically and supplied with a sublateral spinicle.

REMARKS

Any obvious troglomorphic traits in this species seem to be absent.

Plusioglyphiulus steineri n. sp. (Figs 14-17)

TYPE MATERIAL. — Laos. Khammouan Prov., Gnommalat, $17^{\circ}37.907'N$, $105^{\circ}07.461'E$, Cave Tham Kamuk, guano, 19.II.2003, leg. H. Steiner, holotype ♂ (VMNH); 2 ♂♂ paratypes, 1 fragment paratype, 2 juveniles paratypes (VMNH). — Same locality, 20.II.2003, 1 ♂, 1 ♀ paratypes (VMNH); 2 ♂♂, 1 ♀ paratypes (MNHN GA058); 1 ♂ paratype (ZMUM); 1 ♂ paratype (ZMUC); 1 ♂ paratype (SEM).

ETYMOLOGY. — To honour Helmut Steiner, who collected this material.

DIAGNOSIS. — Differs from congeners by the especially complex gonopod structure, coupled with the isostichic carinotaxy of the collum and of other body segments, the convex paraprocts, the subtrapeziform epiproct and the absence of spots dorsad of the ocellaria.

DESCRIPTION

Length of adults 27-35 mm, width 1.8-2.0 mm, collum and segments of posterior third of body being equally broadest. Coloration usually uniformly grey-brown, sometimes with a paramedian pair of more or less wide, grey-yellowish stripes; collum, head and segment 2 mostly pale; tips of tergal crests/tubercles usually dark brown; ocellaria dark brown to blackish, devoid of adjacent spots dorsally.

Body with $56-69p+2-1a+T$. Length of holotype about 27 mm, width 1.8 mm, with $56p+1a+T$.

Antennae rather elongate (Figs 14A; 17A), antennomeres 6 and 7 each with a considerable group of bacilliform sensilla distodorsally; similar but minute sensilla present also on antennomere 7. Ocellaria transversely subreniform, with 9-12 ocelli in 5-7 longitudinal rows. Gnathochilarium oligotrichous (Fig. 17B).

Postcollar constriction very evident, collum and segment 2 being strongly enlarged (Fig. 14B). Carinotaxy formula of collum: $I+//t+2p/t+3p/t+4p/t+ta/t+6p/t/t+7a/t+pp/t+ma/t$ (Fig. 14A, B). Carinotaxy of metatergum 2, $8/8+m/m+8/8$; formula of metaterga 3 and 4, $7/7+M(m/m)+7/7$, dorsal $3+3$ tubercles in anterior row being subtransverse; formula of metatergum 5, $3/3+I/i+3/3+m/m+3/3+I/i+3/3$; formula of subsequent metaterga, $3/3+I/i+3/3+3+m/m(m/m/m)+3/3+I/i+3/3$; that of apodous segments, $7/7+m/m+7/7$ (Fig. 14); all

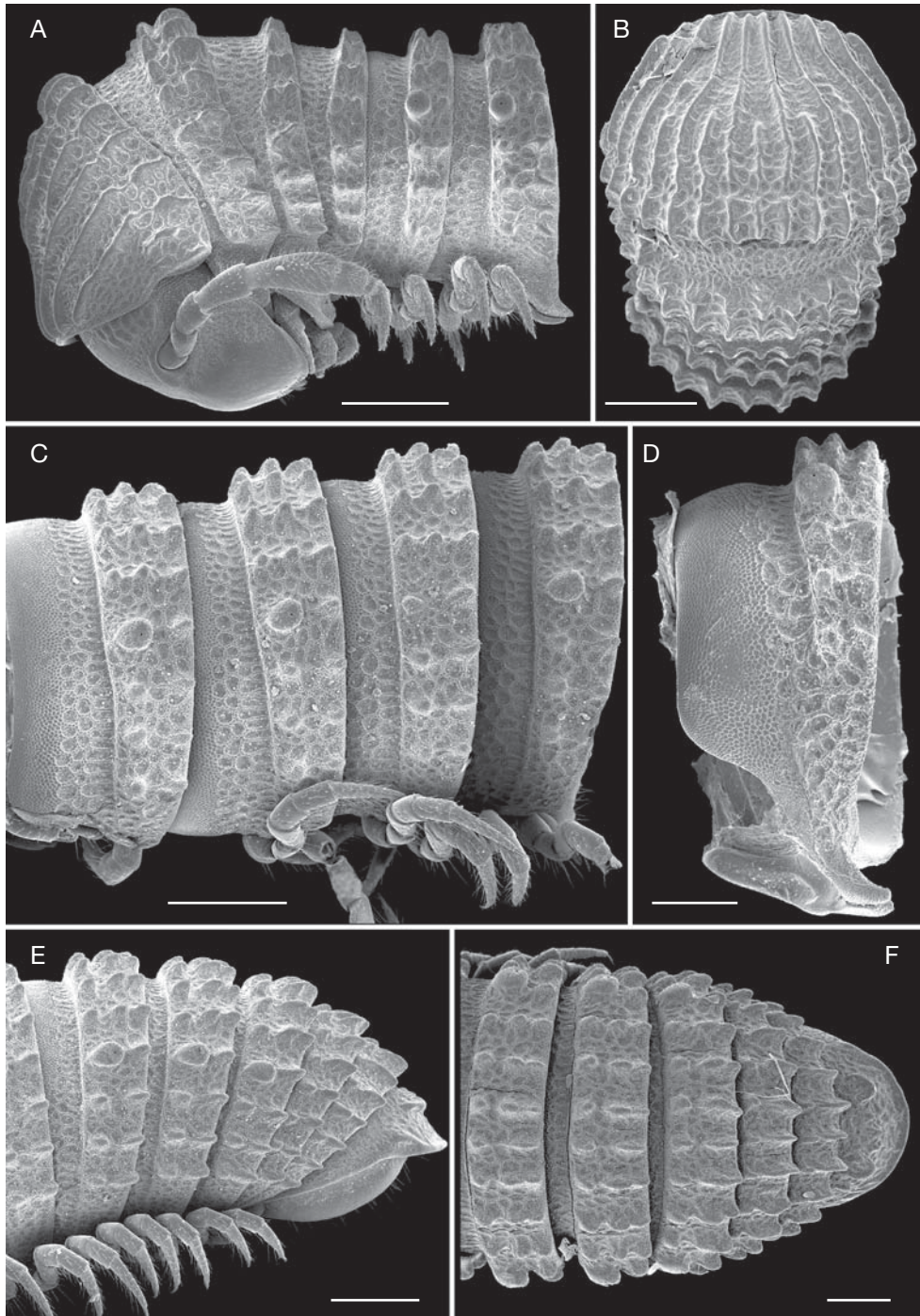


FIG. 14. — *Plusioglyphiulus steineri* n. sp., paratype ♂: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, midbody segments, lateral view; **D**, segment 7, ventrolateral view; **E**, posterior part of body, lateral view; **F**, same, dorsal view. Scale bars: A-C, E, F, 0.5 mm; D, 0.2 mm.

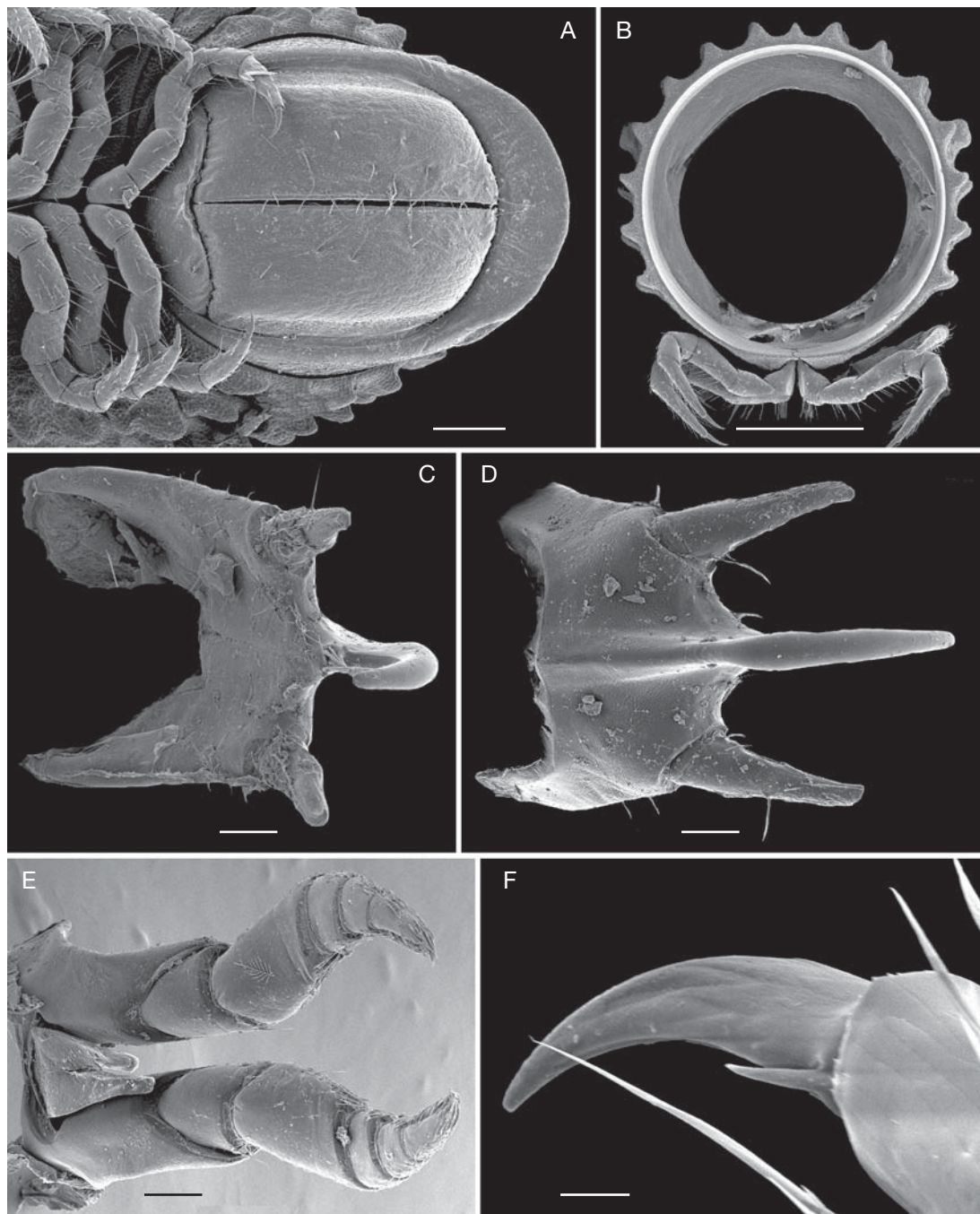


FIG. 15. — *Plusioglyphiulus steineri* n. sp., paratype ♂: **A**, telson, ventral view; **B**, midbody segment section; **C**, leg 1, frontoventral view; **D**, same, caudal view; **E**, leg 2, caudal view; **F**, claw of midbody leg. Scale bars: A, 0.2 mm; B, 0.5 mm; C-E, 0.1 mm; F, 0.01 mm.



FIG. 16. — *Plusioglyphiulus steineri* n. sp., paratype ♂: **A**, anterior gonopods, frontal view; **B**, same, caudal view; **C**, posterior gonopods, frontal view; **D**, same, caudal view. Abbreviations: **cxp**, coxal process; **d**, flagelliform arm; **te**, telopodite; **x**, **y**, dentiform flaps. Scale bars: 0.1 mm.

crests and tubercles rather high, poriferous cones (I) only slightly higher, and median ones (m) slightly lower, than others (Figs 14A-E; 15B). Dorsal crests

on several posteriormost segments considerably higher than others (Fig. 14E). Midbody segments circular in cross-section (Fig. 15B). Pleural regions

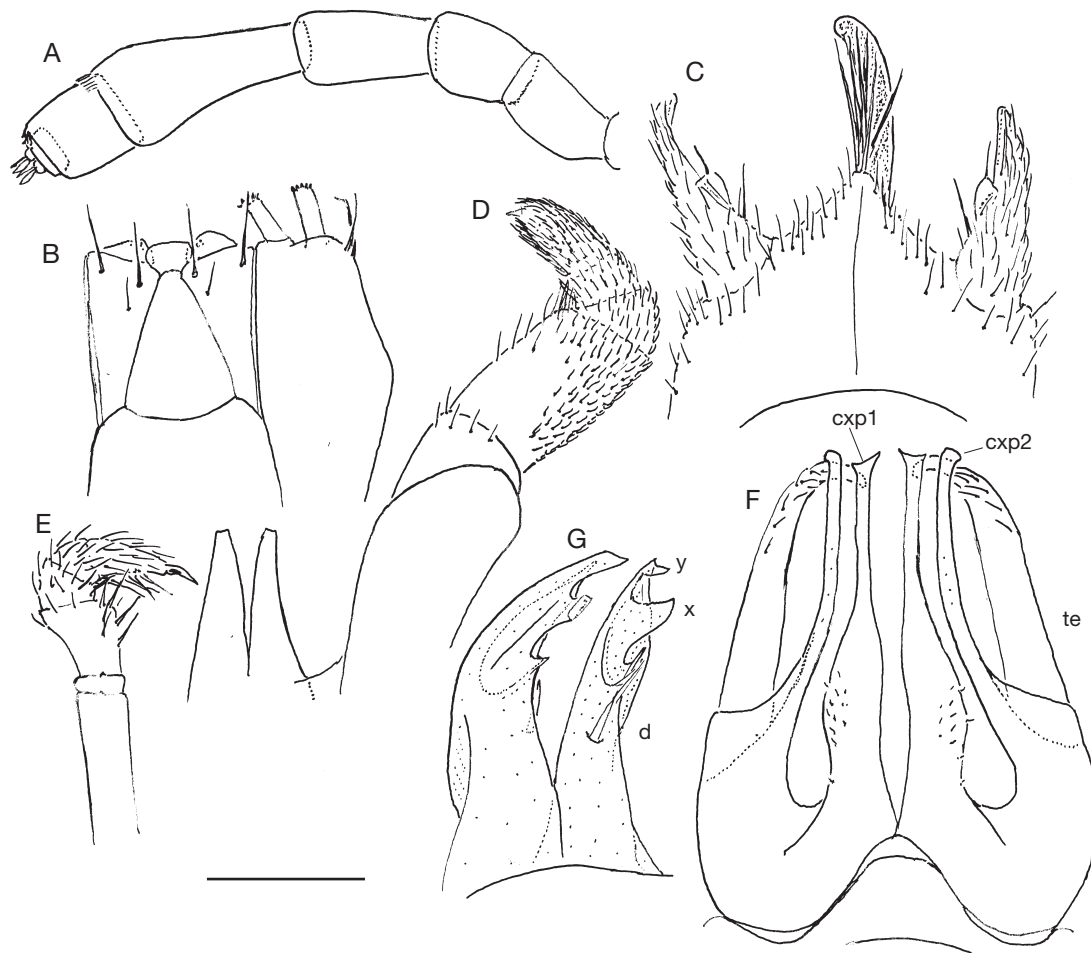


FIG. 17. — *Plusioglyphiulus steineri* n. sp., paratype ♂: **A**, antenna, lateral view; **B**, gnathochilarium; **C**, leg 1, frontal view; **D**, leg 2, frontal view; **E**, leg 3, frontal view; **F**, anterior gonopods, frontal view; **G**, posterior gonopods, frontolateral view. Abbreviations: **cxp**, coxal process; **d**, flagelliform arm; **te**, telopodite; **x**, **y**, dentiform flaps. Scale bar: 0.3 mm.

of segments 2–4 conspicuously expanded, flap-shaped, especially so on segment 3 (Fig. 14A). Pleural ridge behind gonopod aperture on male segment 7 (Fig. 14D), tegument and limbus as in above congeners. Epiproct regularly and broadly rounded apically, with a small median knob and 1+1 unusually high, paramedian, subtransverse tubercles at midway; paraprocts flattened; hypoproct emarginate at caudal margin (Figs 14E, F; 15A).

Legs short, on midbody segments about half as long as body diameter (Fig. 15B). Claw at base with a strong but relatively short accessory spine

about $\frac{1}{4}$ as long as claw itself (Fig. 15F). Tarsi, tarsal setae and male legs 1–3 (Figs 15C–E; 17C–E) as in *P. grandicollis*, but a rudimentary telopodite of male leg 1 persisting as a knob.

Anterior gonopods (Figs 16A, B; 17F) much like in *P. ampullifer* n. sp., but processes cxp1 non-contiguous, very slender and high, with short pilosity laterally near base, subsecriform apically; processes cxp2 very slightly curved, similarly slender and high; telopodites (te) simple, laterocaudal in position, movable, high, subcylindrical, setose in distal third, apically curved mesad. Posterior gonopods (Figs 16C, D; 17G) small,

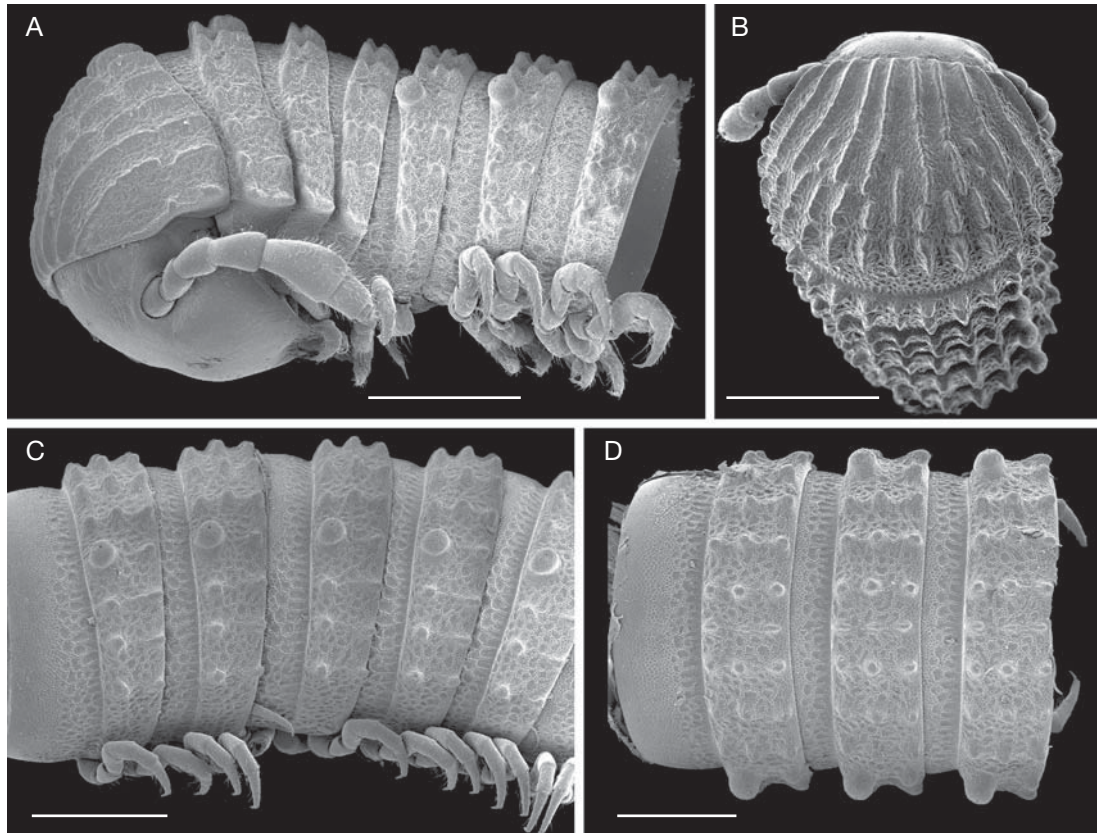


FIG. 18. — *Plusioglyphiulus deharvengi* n. sp., paratype ♀: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, midbody segments, lateral view; **D**, same, dorsal view. Scale bars: 0.5 mm.

complex, resembling a pair of curved forceps, without traces of telopodites; each coxite crescent-shaped, attenuating distad, with a rather long and flagelliform arm (d) at about basal third mesally, a shelf-like structure and two dentiform flaps (x and y) on frontal face.

REMARKS

Any obvious troglomorphic traits in this species seem to be absent.

Plusioglyphiulus deharvengi n. sp. (Figs 18-20)

TYPE MATERIAL. — Laos. Luang Prabang Prov., 19.88°N, 102.14°E, Xieng Maen, Cave Vat Tham, by hand,

30.XII.1999, leg. L. Deharveng & A. Bedos (LAO-106), holotype ♂ (MNHN GA059); 1 ♂, 1 ♀ paratypes (MNHN GA059); 1 ♀ paratype (ZMUM); 1 ♀ paratype (SEM).

ETYMOLOGY. — To honour Louis Deharveng, one of the collectors and donors of this material.

DIAGNOSIS. — Differs from congeners by certain details of gonopod structure (complex anterior gonopods versus very simple posterior ones), coupled with the mixostichic carinotaxy of the collum, the isostichic carinotaxy of other body segments, the flattened paraprocts, the elongated and subtrapeziform epiproct and the presence of spots dorsad of the ocellaria.

DESCRIPTION

Length of adults 20-33 mm, width 1.3-1.9 mm, collum and segments of posterior third of body being equally

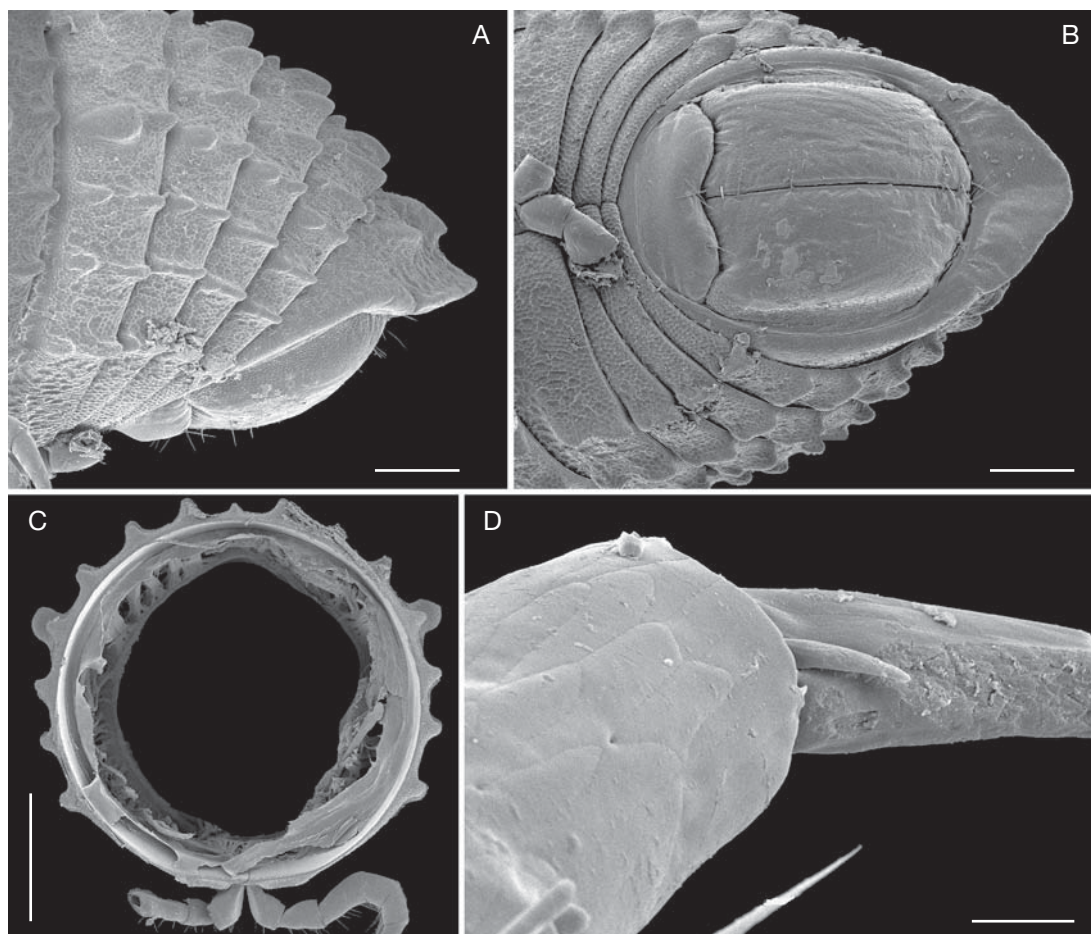


FIG. 19. — *Plusioglyphiulus deharvengi* n. sp., paratype ♀: **A**, posterior part of body, lateral view; **B**, telson, ventral view; **C**, midbody segment section; **D**, claw of midbody leg, subcaudal view. Scale bars: 0.5 mm.

broadest. Coloration usually uniformly yellow-brown, sometimes with a paramedian pair of more or less wide, grey-yellowish stripes; collum, head and segment 2 mostly pale; tips of tergal crests/tubercles usually dark brown; ocellaria brown to blackish, with a pair of adjacent, light brown, well-separated spots dorsally; antennae and distal podomeres light brownish.

Body with 48-59p+4-2a+T. Length of holotype about 33 mm, width 1.9 mm, with 59p+2a+T.

Antennae short and clavate (Fig. 20A), antenno-meres 6 and 7 each with a modest group of bacil-liform sensilla distodorsally. Ocellaria transversely subreniform, with 8-11 ocelli in 5-7 longitudinal

rows. Gnathochilarium oligotrichous, each lamella lingualis with three setae distally.

Postcollar constriction evident, but collum and seg-ment 2 not particularly strongly enlarged (Fig. 18B). Carinotaxy formula of collum slightly variable: ta/t+/(t)/+2p/t+(ta)/(t)+3p/t+4p+ta/t/t+6p/t/t+ta/t+pp/t/t+ma/t (usually), ta/t+2p/t+3p/t/t+ta/t+5p+ta/t+7p/t/t+ta/t+pp/t/t+ma/t or ta/t+2p/t+(ta)/(t)+3p/t+(ta)/(t)+4p+ta/t/t+6p/t/t+ta/t+pp/t/t+ma/t (more rarely) (Fig. 18A, B). Carinotaxy of metatergum 2, 8/8+m/m+8/8; formula of metaterga 3 and 4, 7/7+m/m+7/7; formula of metaterga 5 to 16 and of several segments before apodous, 3/3+1/i+3/3+3+m/

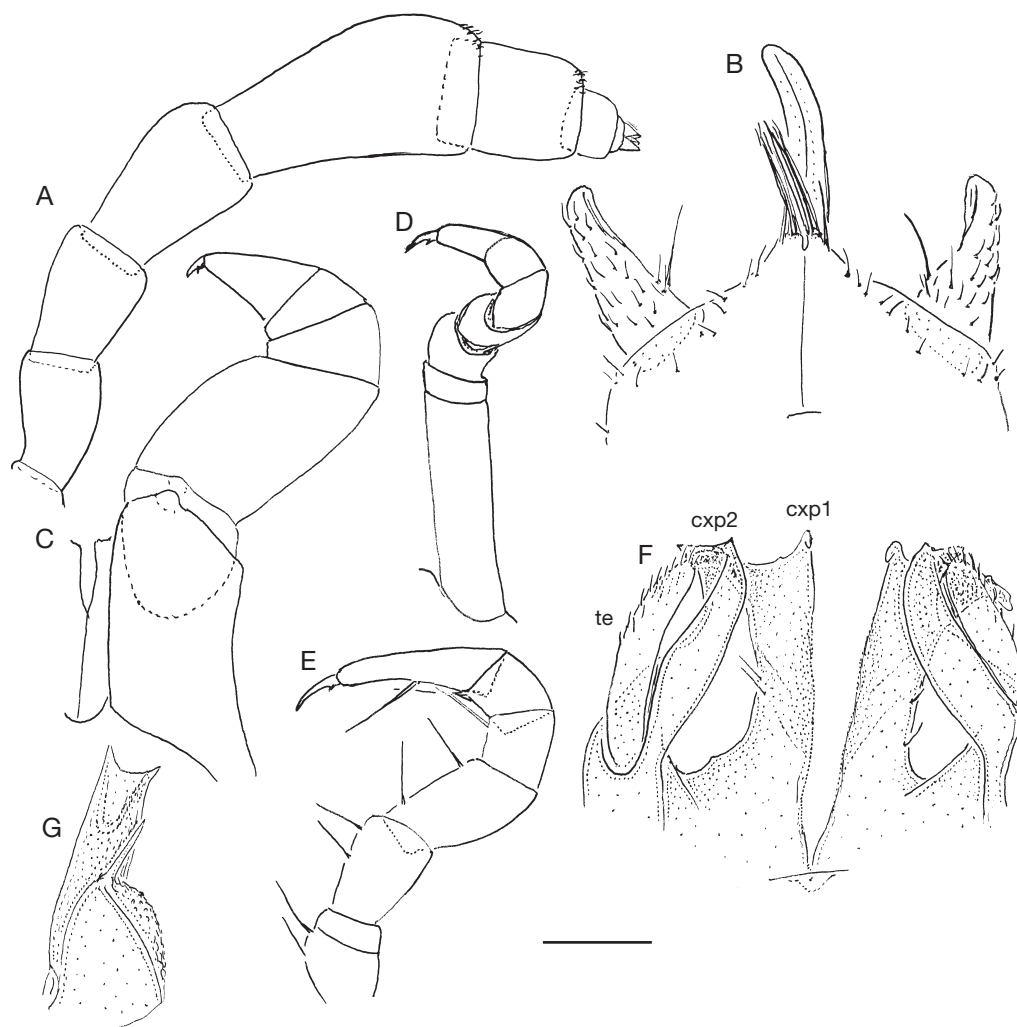


FIG. 20. — *Plusioglyphiulus deharvengi* n. sp., paratype ♂: **A**, antenna, lateral view; **B**, leg 1, frontal view; **C**, leg 2, frontal view; **D**, leg 3, caudal view; **E**, midbody leg; **F**, anterior gonopods, frontal view; **G**, left posterior gonopod, frontal view. Abbreviations: **cxp**, coxal process; **te**, telopodite. Scale bar: 0.2 mm.

$m+3/3/3+I/i+3/3$; formula of midbody metatarga, $3/3+I/i+3/3/3+m/m+3/3/3+I/i+3/3$; that of apodous segments, $4+3/3+m/m+3/3+4$ (Figs 18; 19A); all crests and tubercles rather low, poriferous cones (I) considerably higher, about as high as broad, while median ones (m) lower than others (Figs 18; 19C). Dorsal crests on several posteriormost segments considerably higher than others (Fig. 19A). Midbody segments circular in cross-section (Fig. 19C). Pleural

regions of segments 2–4 conspicuously expanded, flap-shaped, especially so on segment 3 (Fig. 18A). Pleural ridge behind gonopod aperture on male segment 7, tegument and limbus as in above congeners. Epiproct elongate and subtrapeziform apically, with a paramedian pair of high longitudinal crests/tubercles flanked on each side by 1 or 2 small knobs at about midway; paraprocts flattened; hypoproct emarginate at caudal margin (Fig. 19A, B).

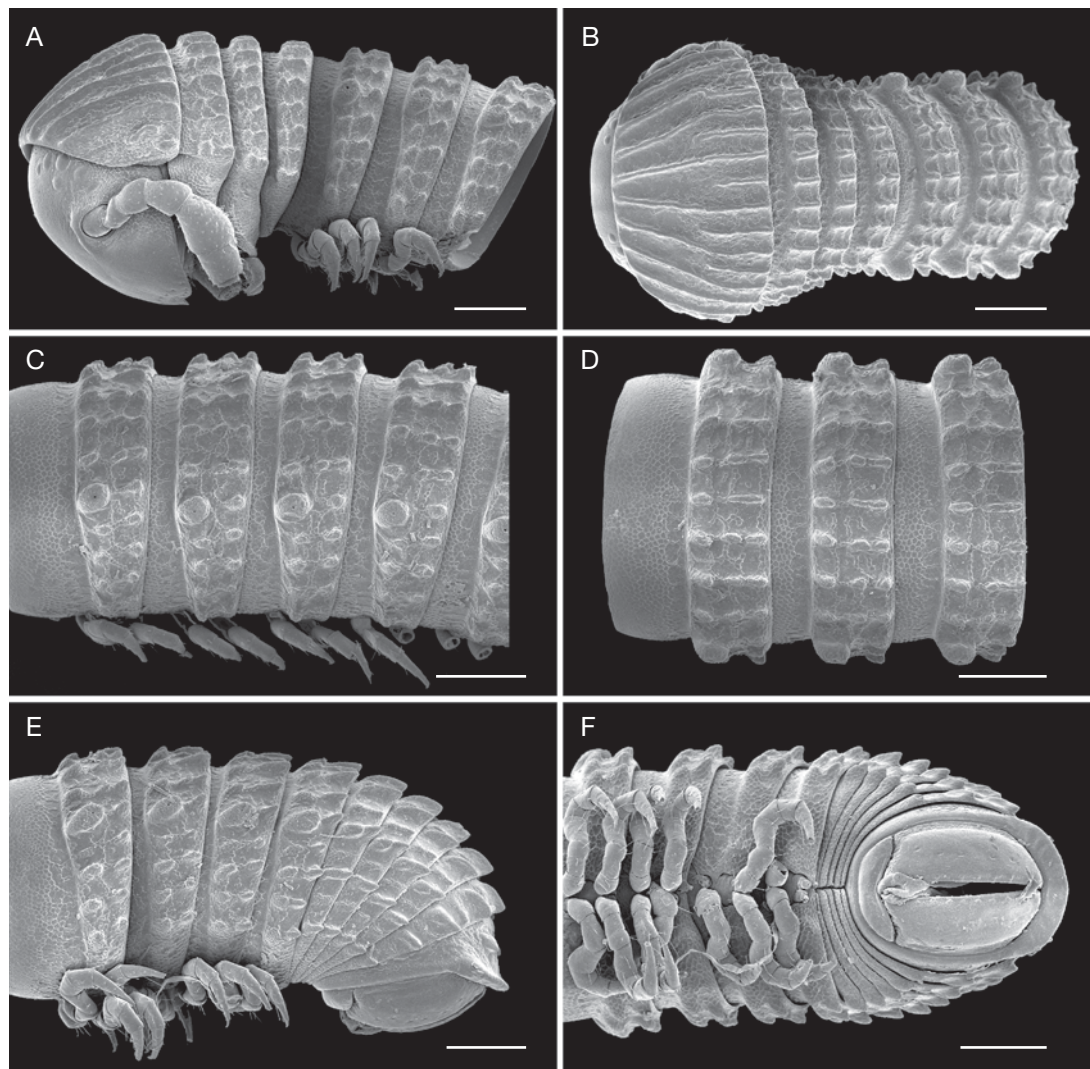


FIG. 21. — *Plusioglyphiulus bedosae* n. sp., paratype ♀: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, midbody segments, lateral view; **D**, same, dorsal view; **E**, posterior part of body, lateral view; **F**, same, ventral view. Scale bars: 0.2 mm.

Legs short and rather stout, on midbody segments about half as long as body diameter (Figs 19C; 20E). Claw at base with a strong but relatively short accessory spine about $\frac{1}{4}$ as long as claw itself (Fig. 19D). Tarsi, their distal setae and male legs 1-3 (Fig. 20B-D) as in *P. grandicollis*.

Anterior gonopods (Fig. 20F) much like in *P. ampullifer* n. sp., but processes cxp1 non-contiguous, lamelliform, broad and high, with a few setae laterally

near base, subsecuriform, terminating in a minute uncus apico-medially and a long, digitiform, slightly curved outgrowth apico-laterally; processes cxp2 of similar shape and length, but retrorse at end; telopodites (te) simple, laterocaudal in position, movable, rather slender and high, subcylindrical, setose in distal half laterally. Posterior gonopods (Fig. 20G) small, simple, without traces of telopodites; each coxite with a rather long, spiniform

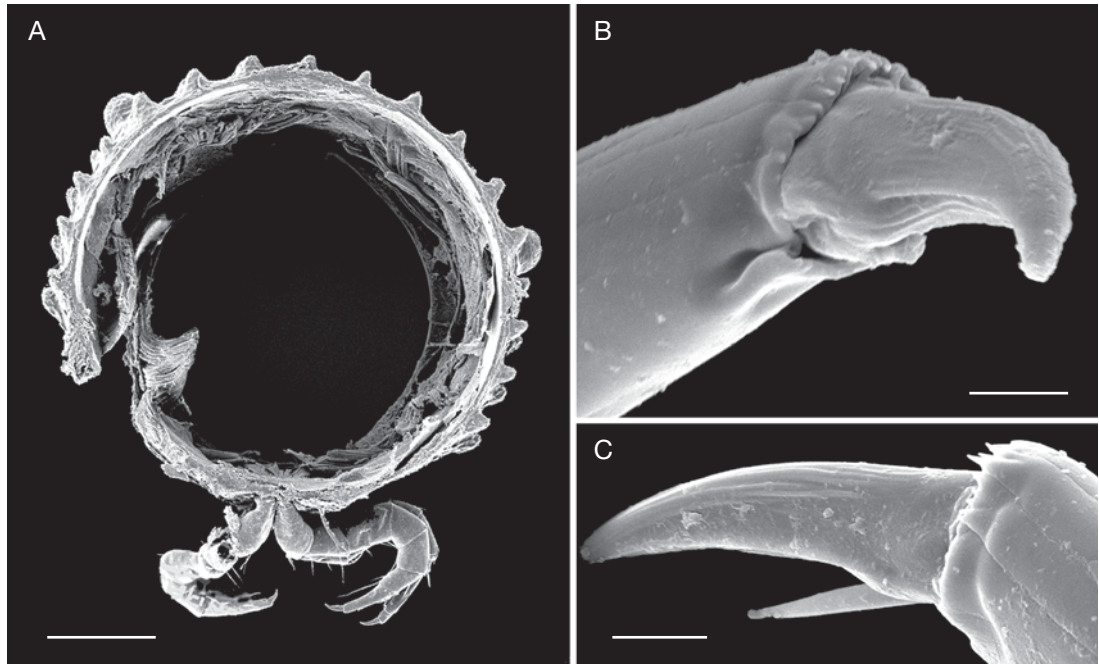


FIG. 22. — *Plusioglyphiulus bedosae* n. sp., paratype ♀: **A**, midbody segment section; **B**, claw, subapical view; **C**, same, subcaudal view. Scale bars: A, 0.2 mm; B, C, 0.005 mm.

arm (d) at about midway on frontal face, distal half lamelliform, parallel-sided, with a deep fovea and a modest emargination apically.

REMARKS

Any obvious troglomorphic traits in this species seem to be absent.

Plusioglyphiulus bedosae n. sp. (Figs 21–23)

TYPE MATERIAL. — **Indonesia**. Borneo, Kalimantan Timur, Kutai Timur, Sangkulirang, Baai, 01.332°N, 117.397°E, Cave Gua Ambulabung, by hand, 15.VIII.2004, leg. A. Bedos & L. Deharveng (KAL-071), holotype ♂ (MZB); 1 ♀ paratype (MNHN GA060), 1 juvenile ♂ paratype (SEM).

ETYMOLOGY. — To honour Anne Bedos, one of the collectors of this material.

DIAGNOSIS. — Differs from congeners in the small size, the particular carinotaxy formulae, coupled with the peculiar structure of male legs 1–3, as well as of the gonopods.

DESCRIPTION

Length of adults about 22 mm, width 1.3 mm, segments of posterior third of body being broadest.

Coloration generally marbled grey-brown, with two broad, paramedian, grey-yellowish, more or less distinct stripes dorsally and with brown prozona, thus providing a cingulate pattern; collum and segment 2 mostly yellow to light brown; head mostly pale brown to brown, at least dorsad of interantennal isthmus, with a yellow clypeus; ocellaria blackish; antennae dark brown, distal podomeres light brown to brown.

Body of adults with 52p+2a+T (holotype) or 51p+3a+T (paratype).

Antennae short and clavate (Figs 21A; 23A), antennomeres 5 and 6 each with a small group of bacilliform sensilla distodorsally. Ocellaria transverse, with 11–13, mostly isolated ocelli in 5 or 6 longitudinal rows. Gnathochilarium oligotrichous.

Postcollar constriction evident, but collum and segment 2 not particularly strongly enlarged (Fig. 21A, B). Carinotaxy formula of collum:

I+/(t)+/II+III+IV+5a+VI+7a+P+ma (Fig. 21A, B). Carinotaxy of metatergum 2, 4/4+4+M+4+4/4; formula of metaterga 3 and 4, 8/8+m/m+8/8; formula of metaterga 5 to several before apodous, 4/4+I/i+3/3/3+m/m+3/3/3+I/i+4/4; formula of several caudal metaterga in front of apodous, 4/4+I/i+3/3+m/m+3/3+I/i+4/4; that of apodous segments, 3+1/1+3+M+3+1/1+3 (Fig. 21A-E); all crests and tubercles rather low, poriferous cones (I) slightly higher, broader than high, while median ones (m) slightly lower than others (Fig. 22A). Dorsal crests on several posteriormost segments considerably higher than others (Fig. 21E). Midbody segments circular in cross-section (Fig. 22A). Pleural regions of segments 2-4 conspicuously expanded, flap-shaped, especially so on segment 3 (Fig. 21A). Pleural ridge behind gonopod aperture on male segment 7, tegument and limbus as in above congeners. Epiproct regularly rounded apically, with a paramedian pair of evident, caudally converging tubercles at about midway; paraprocts flattened; hypoproct emarginate at caudal margin (Fig. 21E, F).

Legs short, rather stout, on midbody segments about half as long as body diameter (Figs 22A; 23E). Claw at base with a strong accessory spine about half as long as claw itself (Figs 22B, C; 23E). Tarsi and their distal setae as in other congeners.

Male coxae 1 (Fig. 23B) subconical, strongly reduced and shorter than central sternal uncus. Male telopodites 2 (Fig. 23C) not particularly incrassate, with an elongated tarsus. Male telopodites 3 (Fig. 23D) only slightly reduced compared to elongated coxae.

Anterior gonopods (Fig. 23F, G) much like in *P. ampullifer* n. sp., processes cxp1 contiguous medially, lamellate, digitiform, very finely fringed apically, shorter than processes cxp2; latter also lamellate, elongate and subacuminate, almost in touch near apex; telopodites (te) simple, laterocaudal in position, movable, rather slender and high, subcylindrical, setose on caudal face. Posterior gonopods (Fig. 23H) small, simple, without traces of telopodites; each coxite with a rather long, rod-shaped, distally micropilose arm (d) at basal third on frontal face, distal part finely fringed apically, lamelliform, nearly parallel-sided, with long lateral and mesal flaps, latter flap being surmounted with a short process.

REMARKS

This is a rather atypical member of *Plusioglyphiulus*. It deviates chiefly in the somewhat more plesiomorphic characters of both male legs 2 and 3, but, on account of the increased number of metatergal tubercles and collar crests, as well as the overall gonopod conformation, its assignment to this genus seems preferable for the moment.

Any obvious troglomorphic traits in this species seem to be absent.

Plusioglyphiulus pallidior n. sp. (Figs 24-26)

TYPE MATERIAL. — **Indonesia**. Borneo, Kalimantan Timur, Kutai Timur, Sangkulirang, Baai, 01.332°N, 117.397°E, Cave Gua Ambulabung, by hand, 14.VIII.2004, leg. A. Bedos & L. Deharveng (KAL-068), holotype ♂ (MZB); 2 subadult ♂♂ paratypes (MZB); 1 ♂, 1 ♀ paratypes (MNHN GA061). — Same cave, 15.VIII.2004, leg. A. Bedos & L. Deharveng (KAL-071), 1 ♂ paratype (ZMUM). — Deep part of the same cave, by hand, 16.VIII.2004, leg. A. Bedos & L. Deharveng (KAL-110), 1 subadult ♀ paratype (MNHN GA061); 1 juvenile ♀ paratype (SEM).

ETYMOLOGY. — To emphasize the lighter general coloration compared to the sympatric and even syntopic *P. bedosae* n. sp.

DIAGNOSIS. — Differs from congeners by certain details of gonopod structure (unusually enlarged anterior gonopods versus rather slender posterior ones), coupled with the mixostichic carinotaxy of the collum and of other body segments, the presence of a marked depression on the collum and of only two rows of bituberculate crests below the poriferous cones on most of the body segments, the flattened paraprocts, the short and broadly rounded epiproct and the absence of spots dorsad of the ocellaria.

DESCRIPTION

Length of adults 43-50 mm, width 2.0-2.1 mm, segments of posterior third of body being broadest. Coloration uniformly light yellow-brown; head (except for blackish ocelli), collum and segments 2-7 entirely yellow.

Body of adults with 64-70p+2-1a+T. Length of holotype about 50 mm, width 2.1 mm (width of collum, 2.0 mm) with 70p+2a+T.

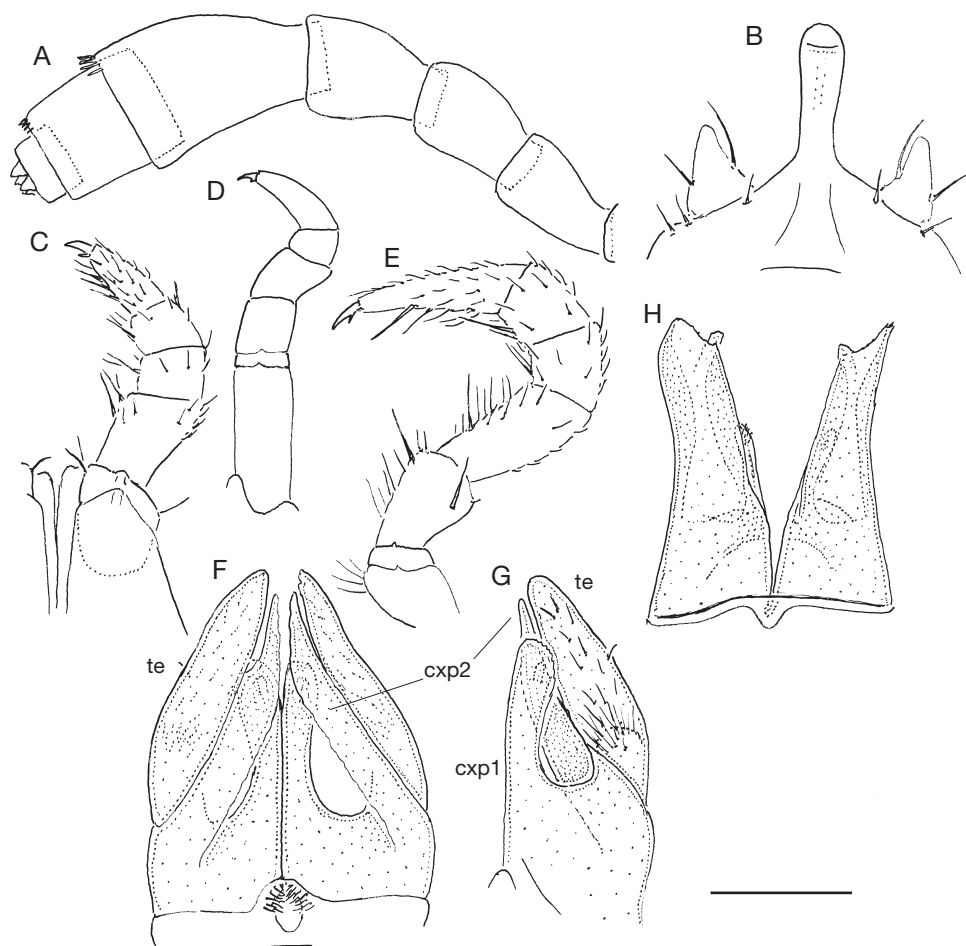


FIG. 23. — *Plusioglyphiulus bedosae* n. sp., paratype ♂: **A**, antenna, lateral view; **B**, leg 1, frontal view; **C**, leg 2, frontal view; **D**, leg 3, caudal view; **E**, leg 11; **F**, anterior gonopods, frontal view; **G**, right anterior gonopod, caudal view; **H**, posterior gonopods, caudal view. Abbreviations: **cxp**, coxal process; **te**, telopodite. Scale bar: 0.2 mm.

Clypeus with 3 ($n = 2$) or 5 teeth ($n = 1$) antero-medially. Antennae short and clavate (Fig. 26A), antennomeres 6 and 7 each with a very considerable group of bacilliform sensilla distodorsally. Ocellaria transversely subtriangular, with 8-11 ocelli in 5-7 longitudinal rows. Gnathochilarium oligotrichous (Fig. 26B).

Postcollar constriction very evident, collum and segment 2 particularly strongly enlarged (Fig. 24A). Carinotaxy formula of collum variable: $ta/t+2p/t+3p/t/t+t+///(t)+4p/t/t+t+5p/t/t+pp/t/t+t+//ma/t$ or $//t+2p/t/t+3p/t/t+4p/t/t+t+/(ta)/(t)+5p/t/t+pp/t/t+t+ma/t$ (Fig. 24A). Collum strongly depressed near

anterior third (Fig. 24A). Carinotaxy of metatergum 2, $6/6+m/m+6/6$; formula of metaterga 3 and 4, $3/3+3+M+3+3/3$; formula of metaterga 5-7 and of several segments before apodous, $2/2+I/i+3/3+m/m+3/3+I/i+2/2$; formula of midbody metaterga, $2/2+I/i+3/4/3+m//m+3/4/3+I/i+2/2$ in adults, $2/2+I/i+3/3+m/m+3/4/3+I/i+2/2$ in subadults; formula of apodous segments, $4+0+4$ (Figs 24; 25A); all crests and tubercles rather high, poriferous cones (I) considerably higher, about as high as broad, while median ones (m) slightly lower than others (Fig. 24B). All tergal tubercles microgranular (Fig. 25C). Dorsal crests on several posteriormost segments considerably

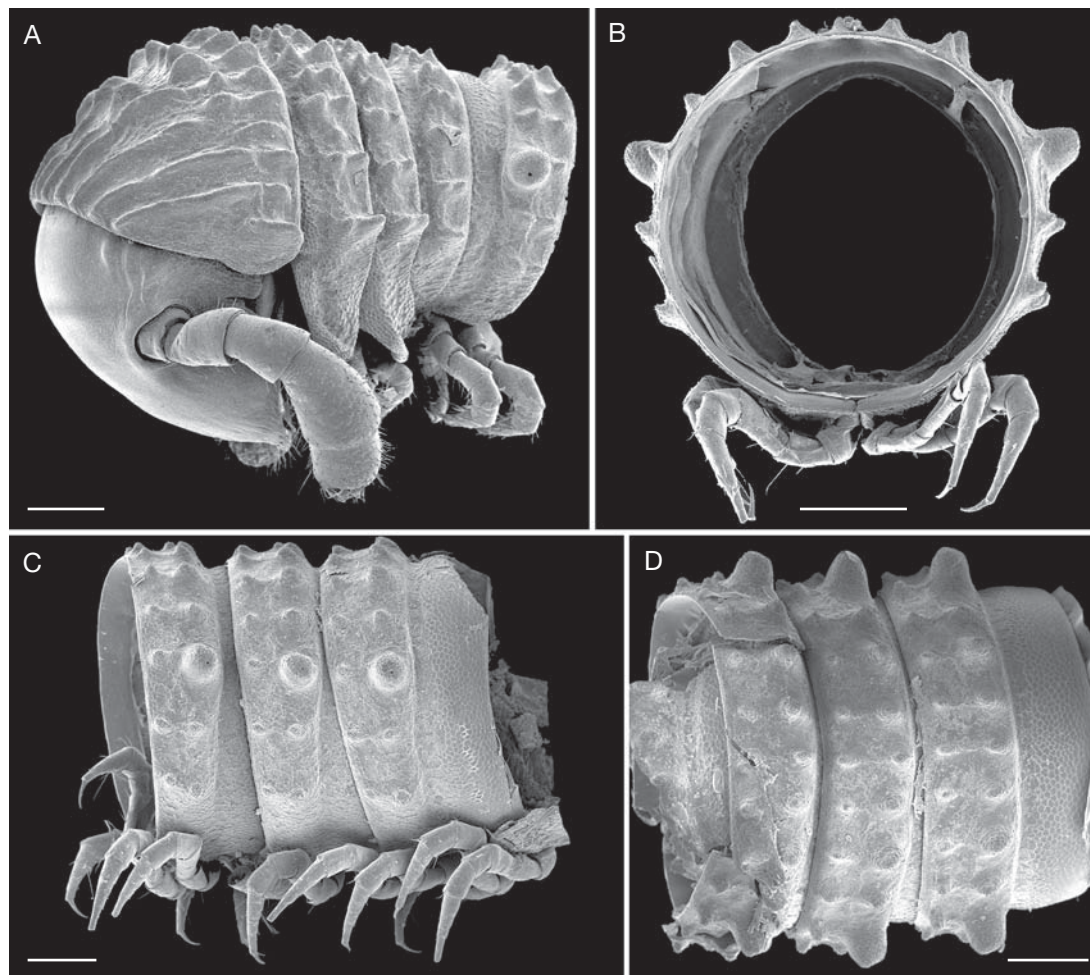


FIG. 24. — *Plusioglyphiulus pallidior* n. sp., paratype juvenile ♀: **A**, anterior part of body, lateral view; **B**, midbody segment section; **C**, midbody segments, lateral view; **D**, same, dorsal view. Scale bars: 0.2 mm.

higher than others (Fig. 25A). Midbody segments circular in cross-section (Fig. 24B). Pleural regions of segments 2–4 conspicuously expanded, flap-shaped, especially so on segment 3 (Fig. 24A). Pleural ridge behind gonopod aperture on male segment 7, tegument and limbus as in above congeners. Epiproct short, regularly and broadly rounded apically, with a paramedian pair of high but short crests/tubercles sometimes flanked on each side by 1 or 2 small knobs at about midway; paraprocts flattened; hypoproct emarginate at caudal margin (Fig. 25A, B).

Legs relatively long, on midbody segments about $\frac{3}{4}$ as long as body diameter (Fig. 24B). Claw at base

with a very short accessory spine (Fig. 25D). Tarsi and their distal setae as in other congeners. Male legs 1–3 (Fig. 26C–E) more or less as in *P. grandicollis*, but male coxa 1 relatively short, while male telopodite 3 not so compact.

Anterior gonopods (Fig. 26F) generally like in *P. ampullifer* n. sp., but coxites swollen and stout, non-contiguous medially; processes cxp1 very short, beak-shaped, finely ribbed apically; processes cxp2 high, hyaline, subspatuliform, setose at base on frontal face; telopodites (te) simple, lateral in position, movable, rather stout, subcylindrical with tip curved mesad, setose at about midway in distal half laterally.

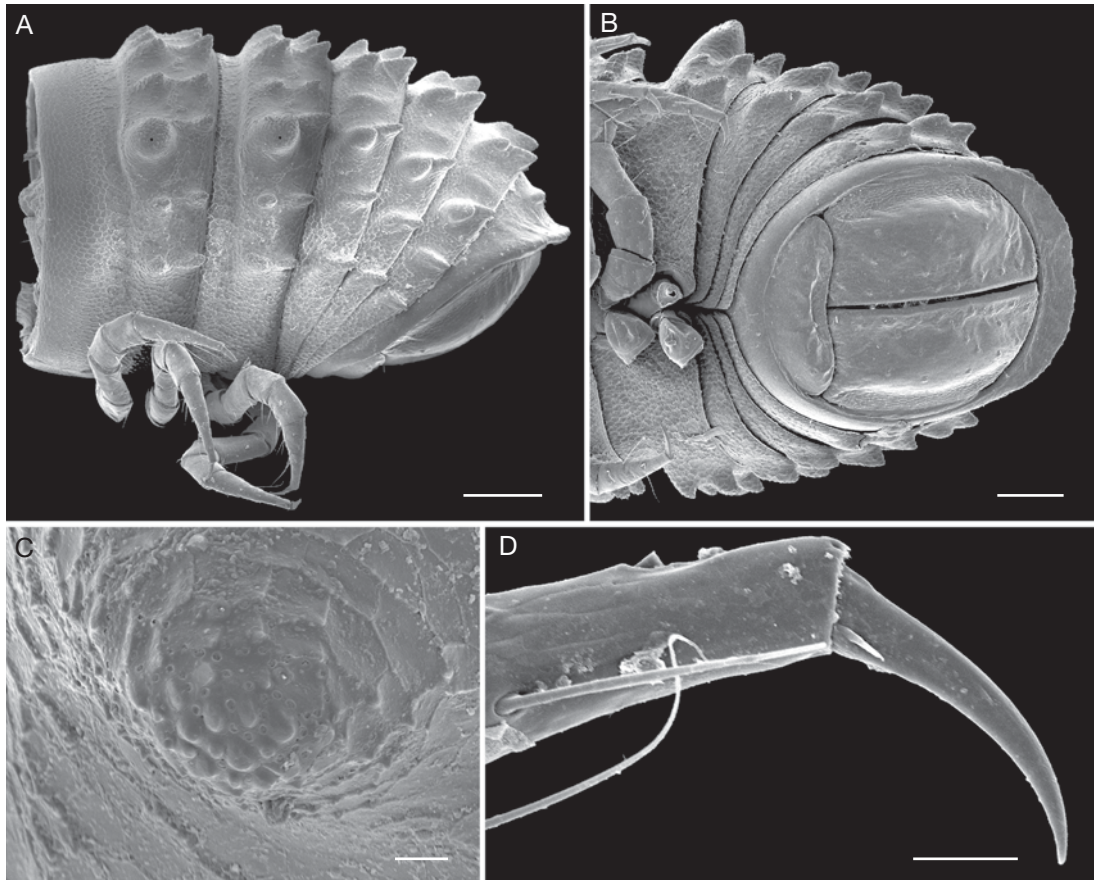


FIG. 25. — *Plusioglyphiulus pallidior* n. sp., paratype juvenile ♀: **A**, posterior part of body, lateral view; **B**, same, ventral view; **C**, texture of tubercle of midbody segment; **D**, claw of midbody leg. Scale bars: A, 0.2 mm; B, 0.1 mm; C, 0.01 mm; D, 0.02 mm.

Posterior gonopods (Fig. 26G) small, relatively simple, without traces of telopodites; each coxite with a long, spiniform arm (d) laterally and a shelf-like structure at about midway on frontal face; distal half lamellose, fringed and with a deep fovea apically.

Subadults about 26 mm long, 1.3 mm wide, pallid, with 53-55p+4a+T and 3-5 blackish ocelli in 2-4 longitudinal rows. Male legs 1 similar to adult condition, but central sternal hook nearly straight, non-unciform. Male legs 2 and 3 slightly less strongly modified than in adults.

REMARKS

The most striking observation obtained from the above material is that an additional, middle row of intercalary tubercles on the metaterga (like in

Fig. 27C, D) seems to appear only at the onset of adulthood.

Any obvious troglomorphic traits in this species seem to be absent. The size differences between *P. bedosae* n. sp. and *P. pallidior* n. sp. are so extreme that niche segregation is strongly suggested, such is the case in some other soil- or cave-dwelling millipedes (Enghoff 1992; Enghoff *et al.* 1997). This is so far the only locality known that supports two species of *Plusioglyphiulus*. That we deal with two different species is beyond any doubt. Even the subadults of *P. pallidior* n. sp. are considerably larger than the adults of *P. bedosae* n. sp. In addition, they differ in gonopod structure so drastically that one (*P. pallidior* n. sp.) could hardly be seen as an ontogenetic derivative of the other (*P. bedosae* n. sp.).

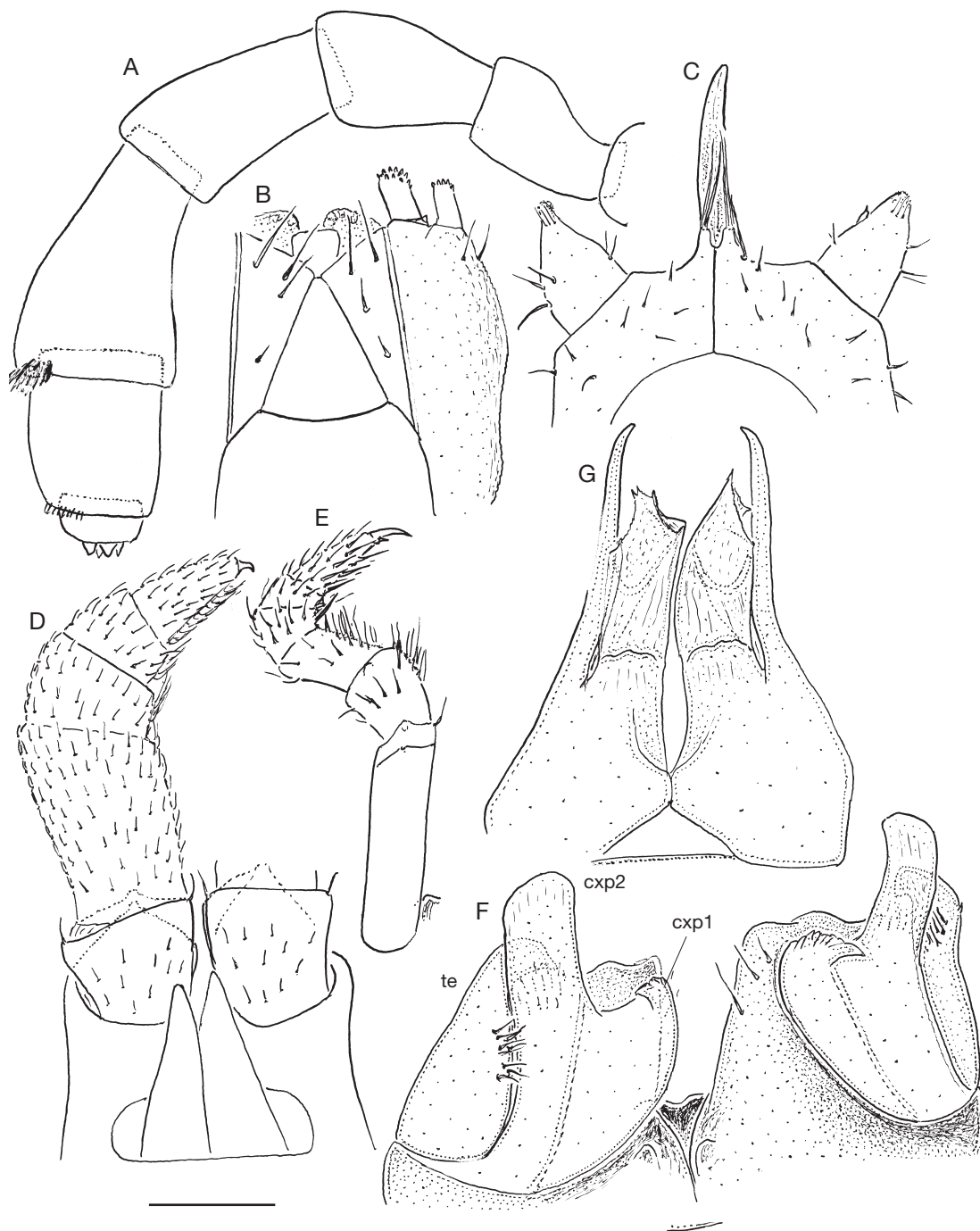


FIG. 26. — *Plusioglyphiulus pallidor* n. sp., paratype ♂: **A**, antenna, lateral view; **B**, gnathochilarium, ventral view; **C**, leg 1, frontal view; **D**, leg 2, caudal view; **E**, leg 3, frontal view; **F**, anterior gonopods, caudal view; **G**, posterior gonopods, frontal view. Abbreviations: **cxp**, coxal process; **te**, telopodite. Scale bar: A-E, 0.4 mm; F, G, 0.2 mm.

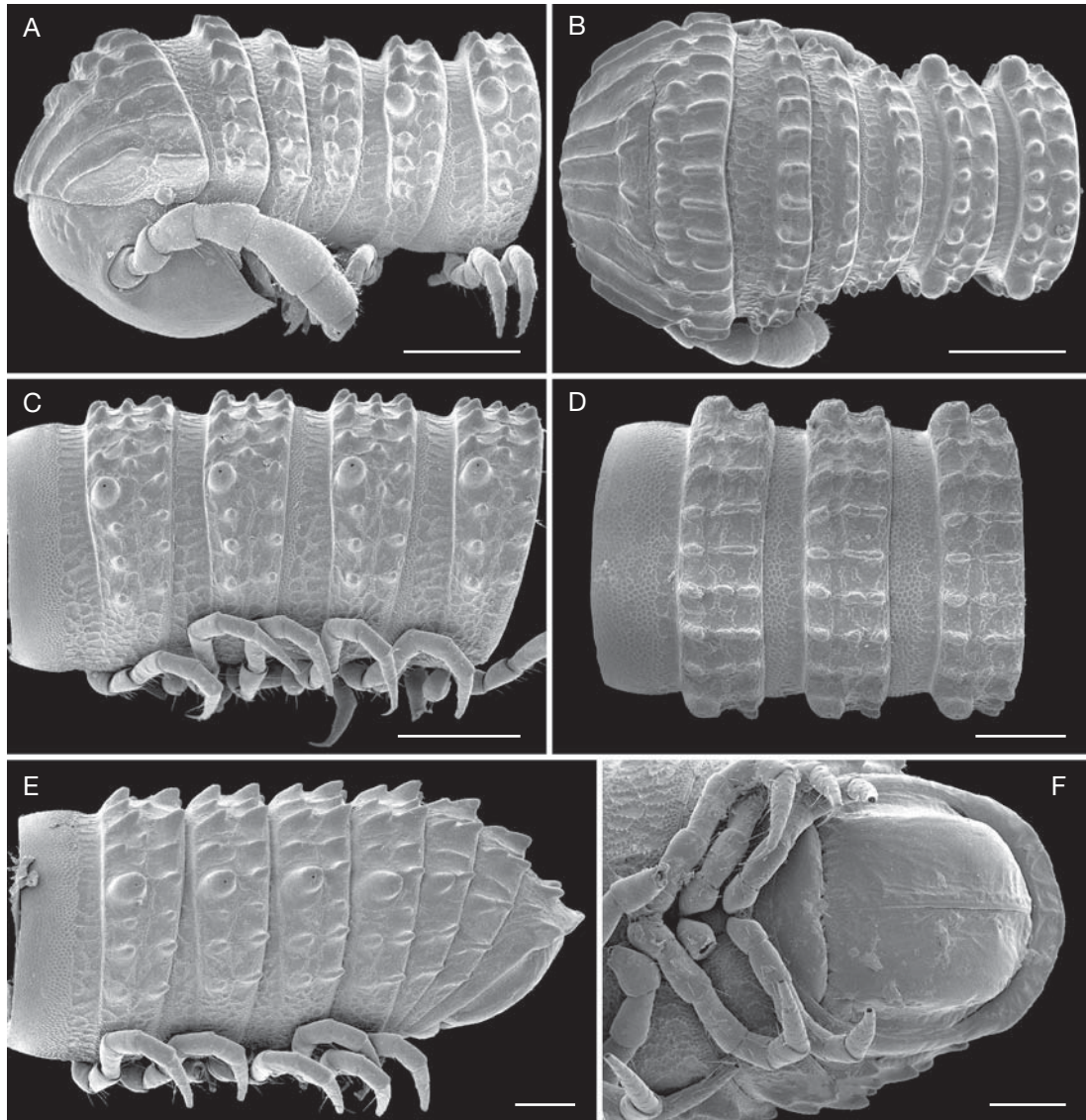


FIG. 27. — *Plusioglyphiulus similis* n. sp., paratype ♂: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, midbody segments, lateral view; **D**, same, dorsal view; **E**, posterior part of body, lateral view; **F**, same, ventral view. Scale bars: 0.2 mm.

Plusioglyphiulus similis n. sp.
(Figs 27-30)

TYPE MATERIAL. — **Indonesia**. Borneo, Kalimantan Timur, Pengadan, 01.257°N, 117.706°E, Cave Gua Ampanas, by hand, 18.VIII.2004, leg. A. Bedos & L. Deharveng (KAL-113), holotype ♂ (MZB); 1 ♂, 1 ♀ paratypes (MNHN

GA062); 1 ♂ paratype (SEM). — Same cave, 18.VIII.2004, leg. Y. R. Suhardjono & C. Rahmadi (KAL-YC04-09), 1 ♀ paratype (MZB); 1 ♂, 1 ♀ paratypes (ZMUM); 1 ♀ paratype (ZMUC); 1 ♀ paratype (VMNH).

ETYMOLOGY. — To emphasize the strong similarities to *P. pallidior* n. sp.

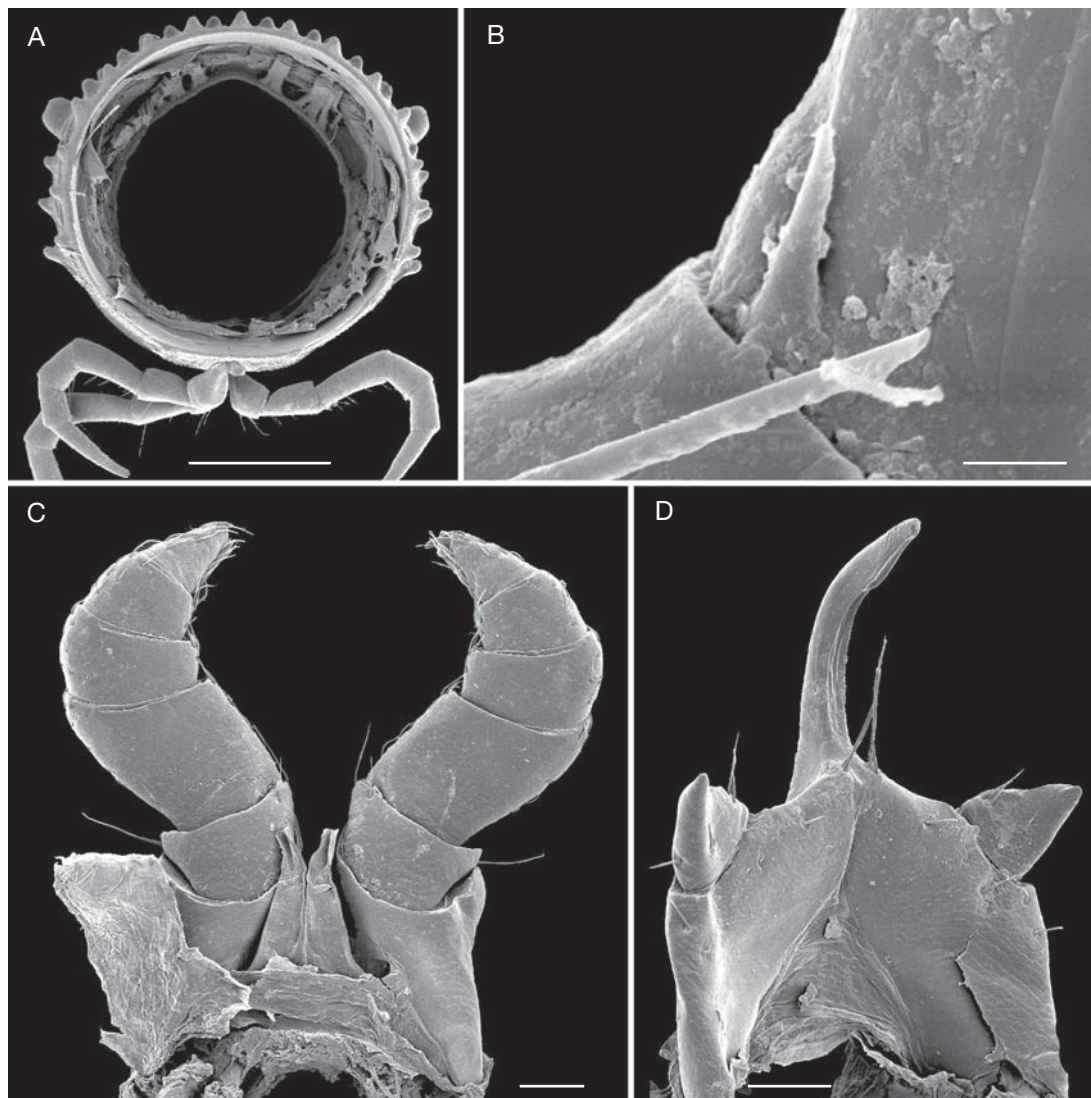


FIG. 28. — *Plusioglyphiulus similis* n. sp., paratype ♂: **A**, midbody segment section; **B**, claw base; **C**, legs 2, frontal view; **D**, legs 1, subfrontal view. Scale bars: A, 0.5 mm; B, 0.005 mm; C, D, 0.1 mm.

DIAGNOSIS. — Differs from the most similar *P. pallidior* n. sp. in the smaller size, the presence of three rows of bituberculate crests below the poriferous cones on most of the body segments and the somewhat longer legs.

DESCRIPTION

Length 17-27 mm, width 1.0-1.6 mm, segments of posterior third of body being broadest.

Coloration marbled brown, sometimes with broad, paramedian, yellow stripes dorsally; head (except for blackish ocelli), collum and segment 2 mostly pale yellow; tips of metaternal tubercles usually brown, those of poriferous tubercles dark brown; antennae and legs light brown.

Body with 42-50p+3-1a+T. Length of holotype about 26 mm, width 1.6 mm, with 50p+1a+T.



FIG. 29. — *Plusioglyphiulus similis* n. sp., paratype ♂: **A**, legs 3, frontal view; **B**, anterior gonopods, frontal view; **C**, same, caudal view; **D**, posterior gonopods, caudal view. Abbreviations: **cxp**, coxal process; **d**, flagelliform arm; **te**, telopodite. Scale bars: A-C, 0.1 mm; D, 0.05 mm.

Antennae rather short and clavate (Figs 27A; 30A), antennomeres 6 and 7 each with a small group of bacilliform sensilla distodorsally. Ocellaria transversely subtriangular, with 8-11 ocelli in 5-7 longitudinal rows. Gnathochilarium slightly more densely setose due to a few small setae on promentum (Fig. 30B).

Postcollar constriction very evident, collum and segment 2 particularly strongly enlarged (Fig. 27A, B). Carinotaxy formula of collum: $1p/t+2p/t+3p/t/t+/(ta)/(t)+4p/t/t+5p/t/t/t+/(ta)/(t)+pp/t/t/t+//ma/t$ (Fig. 27B). Collum slightly depressed near anterior third. Carinotaxy of metatergum 2, $7/7+m/m+7/7$; formula of metaterga 3 and 4, $4/4+3+M+3+4/4$; formula of metaterga 5-7 and of several segments before apodous, $3/3+I/i+3/3+m/m+3/3+I/i+2/2$; formula of midbody metaterga, $3/3+I/i+3/4(5)/3+m//m+3/4(5)/3+I/i+3/3$; that of apodous segments, $4/4+m/m+4/4$ (Fig. 27A-E); all crests and tubercles rather low, poriferous cones (I) considerably higher, but still broader than high, while median ones (m) as high as others (Figs 27A-E; 28A). Dorsal crests on several posteriormost segments considerably higher than others (Fig. 27E). Midbody segments circular in cross-section (Fig. 28A). Pleural regions of segments 2-4 conspicuously expanded, flap-shaped, especially so on segment 3 (Fig. 27A). Pleural ridge behind gonopod aperture on male segment 7, tegument and limbus as in above congeners. Epiproct short, regularly and broadly rounded apically, with a paramedian pair of high but short crests/tubercles sometimes flanked on each side by a small knob at about midway; paraprocts more or less regularly convex, not flattened; hypoproct only slightly emarginate at caudal margin (Fig. 27E, F).

Legs relatively long, on midbody segments about as long as body diameter (Figs 28A; 30F). Claw at base with a short accessory spine (Fig. 28B). Tarsi and their distal setae, as well as male legs 1-3 (Figs 28C, D; 29A; 30C-E) typical.

Both anterior and posterior gonopods (Figs 29B-D; 30G-I) very much like in *P. pallidior* n. sp., but both coxal processes *cxp1* and *cxp2*, and arm (d), slightly different in shape.

REMARKS

Any obvious troglomorphic traits in this species seem to be absent.

Plusioglyphiulus hoffmani n. sp. (Figs 31-33)

TYPE MATERIAL. — **Malaysia.** Borneo, Sarawak, Gunung Mulu National Park, 4.05°N, 114.93°E, Deer Water Cave (Luang Sungai Payau), halfway, in guano, 25.IV.1978, leg. P. J. Chapman, holotype ♂ (VMNH); 3 ♂♂, 5 ♀♀, 1 subadult ♂, 1 subadult ♀ paratypes (VMNH); 1 ♂, 1 ♀ paratypes (MNHN GA063); 1 ♂, 1 ♀ paratypes (ZMUM); 1 ♀ paratype (ZMUC); 1 ♀ paratype (SEM).

ETYMOLOGY. — To honour Richard L. Hoffman (VMNH), a prominent specialist in the systematics of Diplopoda, who provided several samples for this study.

DIAGNOSIS. — Differs from the most similar *P. macfarlanei* Mauriès, 1983 in minor details of gonopod structure (*cxp1* of the anterior gonopod is not extended into a flat lobe, *te* of the same gonopod is recurved and unciform, the apex of the posterior gonopod is less elaborate), the short epiproct, the regularly convex paraprocts and the absence of complete crests on the collum.

DESCRIPTION

Length 19-30 mm, width 1.0-1.6 mm, collum and segments of posterior third of body being equally broadest. Coloration uniformly light yellow-brown to light brown, sometimes with infuscated sides and tips of poriferous tubercles; head (except for brown-blackish ocelli and a paramedian pair of separated, light brown spots dorsad of ocellaria), collum and segment 2 mostly pale yellow; antennae and legs light brown.

Body with $45-53p+3-1a+T$. Length of holotype about 24 mm, width 1.5 mm, with $52p+2a+T$.

Antennae short and clavate (Figs 31A; 33A), antennomeres 6 and 7 each with a considerable group of bacilliform sensilla distodorsally; similar but minute sensilla present also on antennomere 7 (Fig. 32C). Ocellaria transversely subtriangular, with 5-9 ocelli in 4-6 longitudinal rows. Gnathochilarium oligotrichous.

Postcollar constriction very evident, collum and segment 2 particularly strongly enlarged (Fig. 31A, B). Carinotaxy formula of collum: $ta/t+2p/t+3p/t+//ta/t+/(ta)/(t)/(t)+5p/t/t+5p/t/t+//ta/t+pp/t/t/t+//ma/t$ (Fig. 31A, B). Carinotaxy of metatergum 2, $8/8+m/m+8/8$; formula of metaterga 3 and 4, $3/3+4+M+4+3/3$; formula of metaterga 5 and 6, and of several segments before apodous, $3/3+I/i+3/3+m//$

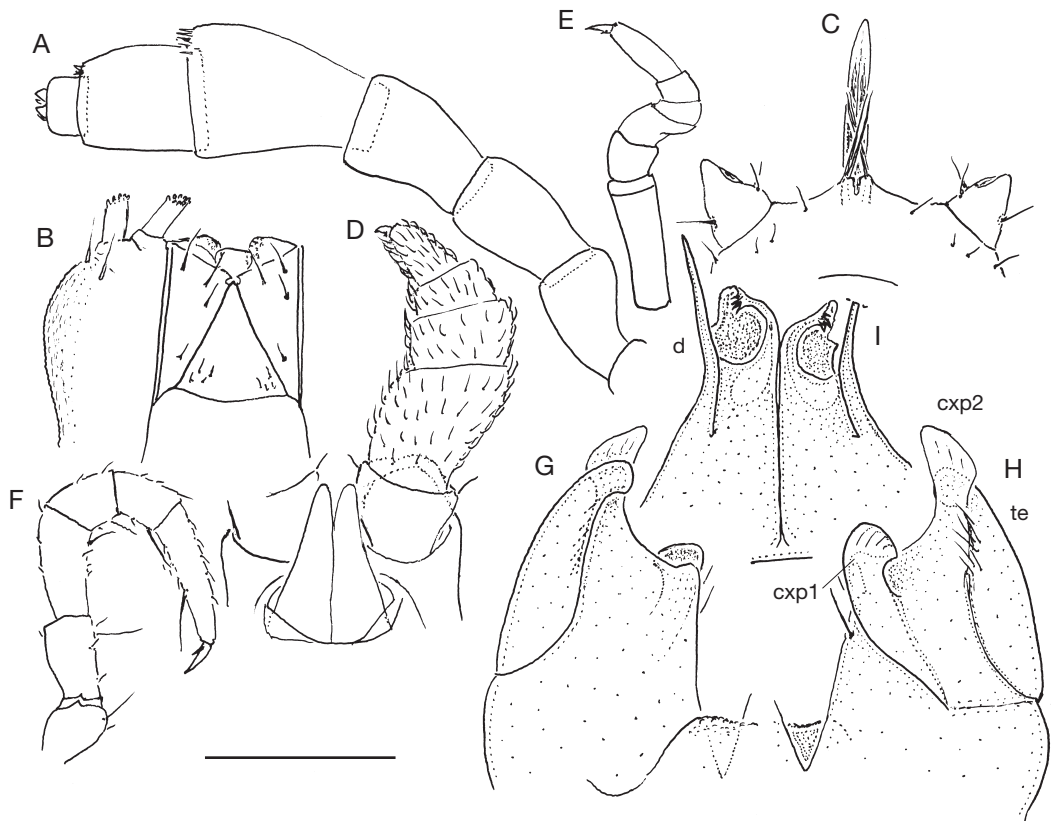


FIG. 30. — *Plusioglyphiulus similis* n. sp., paratype ♂: **A**, antenna, lateral view; **B**, gnathochilarium, ventral view; **C**, legs 1, frontal view; **D**, leg 2, caudal view; **E**, leg 3, frontal view; **F**, leg 11; **G**, left anterior gonopod, frontal view; **H**, same, caudal view; **I**, posterior gonopods, frontal view. Abbreviations: **cxp**, coxal process; **d**, flagelliform arm; **te**, telopodite. Scale bar: A-F, 0.4 mm; G-I, 0.2 mm.

$m+3/3+I/i+3/3$; formula of midbody metaterga, $3/3+I/i+3/4/3+m//m+3/4/3+I/i+3/3$; that of apodous segments, $5+(m)+5$ (Figs 31; 32B); all crests and tubercles rather low, poriferous cones (I) considerably higher, but still broader than high, while median ones (m) as high as others (Figs 31C, D; 32B). Dorsal crests on several posteriormost segments considerably higher than others (Fig. 31E). Mid-body segments circular in cross-section (Fig. 32B). Pleural regions of segments 2-4 conspicuously expanded, flap-shaped, especially so on segment 3 (Fig. 31A). An unusually high, transverse pleural ridge behind gonopod aperture on male segment 7, with very short rounded flaps bent caudad at apex. Tegument and limbus typical. Epiproct very short, subtrapeziform, broadly rounded apically, with a

paramedian pair of well-separated, high but short crests/tubercles at about midway; paraprocts regularly convex, not flattened; hypoproct only slightly emarginate at caudal margin (Figs 31F; 32A).

Legs relatively long, on midbody segments about as long as body diameter (Figs 31C; 33B). Claw at base with a short accessory spine (Figs 32D; 33B). Tarsi and their distal setae, as well as male legs 1-3 as in *P. grandicollis*, *P. ampullifer* n. sp. or *P. pallidior* n. sp.

Anterior gonopods (Fig. 33C) very much like in *P. macfarlanei* in coxites being contiguous but not fused medially, each coxite bearing only a single, laterally serrate, digitiform process (cxp1); telopodites (te) simple, lateral in position, movable, long, likewise digitiform, devoid of setation, with

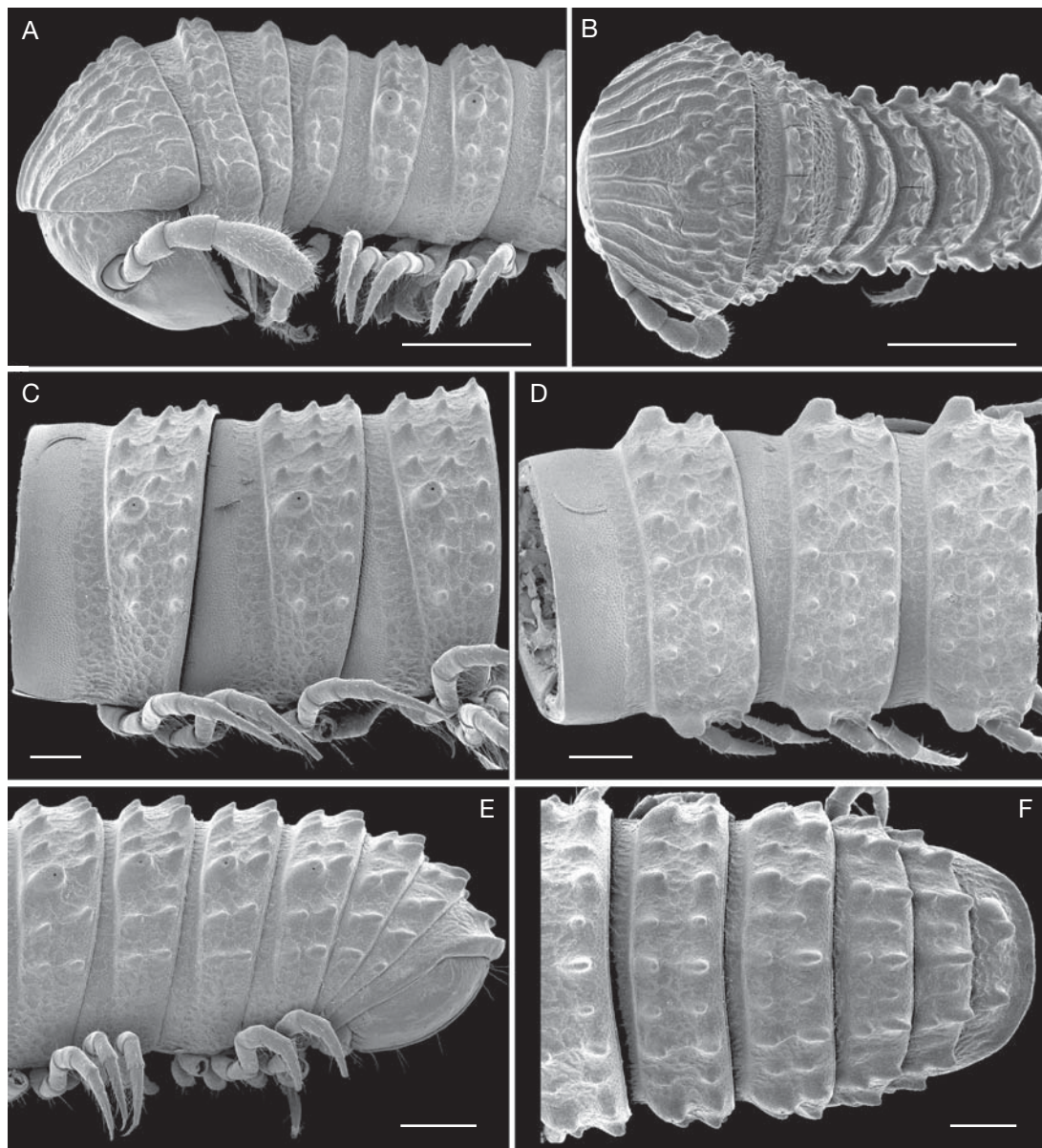


FIG. 31. — *Plusioglyphiulus hoffmani* n. sp., paratype ♀: **A**, anterior part of body, lateral view; **B**, same, dorsal view; **C**, midbody segments, lateral view; **D**, same, dorsal view; **E**, posterior part of body, lateral view; **F**, same, dorsal view. Scale bars: A, B, 0.5 mm; C-F, 0.2 mm.

tip unciform and directed laterad. Posterior gonopods (Fig. 33D) small, relatively simple, without traces of telopodites; each coxite with a very short, rudimentary arm (d) distomedially near a shelf-like

structure; a lobiform tip and a subterminal lateral setoid laterally.

Subadults about 16 mm long, 0.9 mm wide, pallid, with 41-42p+4a+T and three blackish ocelli in two

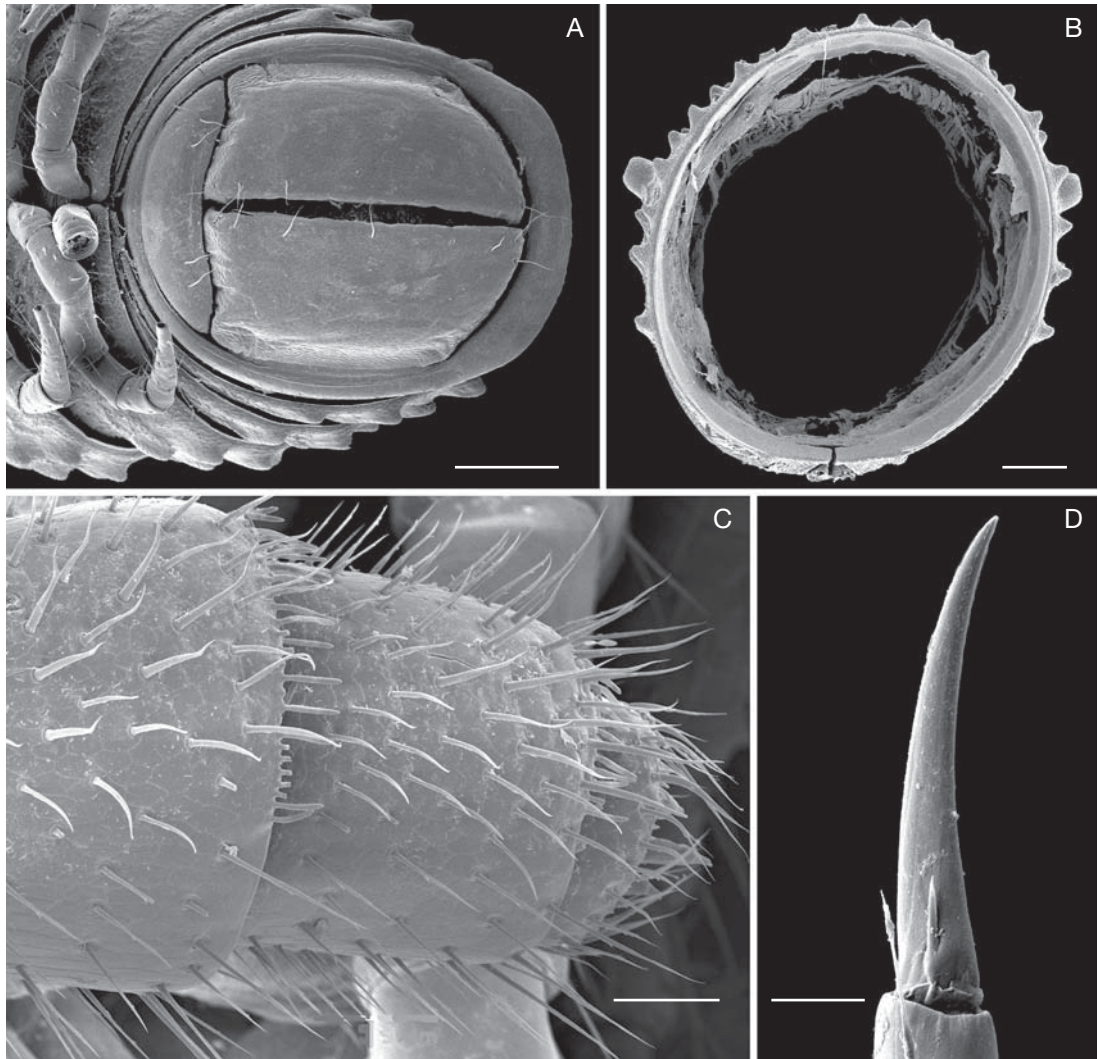


FIG. 32. — *Plusioglyphiulus hoffmani* n. sp., paratype ♀: **A**, telson, ventral view; **B**, midbody segment section; **C**, sensilla on antennomeres 5-7; **D**, claw of midbody leg, subventral view. Scale bars: A, B, 0.2 mm; C, 0.05 mm; D, 0.02 mm.

longitudinal rows. Tubercles of middle, intercalary row on midbody segments very small, rudimentary. Male legs 1 similar to adult condition, but central sternal hook nearly straight, non-unciform. Male legs 2 and 3 slightly less strongly modified than in adults.

REMARKS

Unlike *P. pallidior* n. sp., in which the subadults show no traces of a row of intercalary tubercles on

the midbody segments, the subadults of *P. hoffmani* n. sp. do have such tubercles, albeit strongly reduced in size. In this case these tubercles can be presumed as appearing not at, but towards the onset of adulthood.

Any obvious troglomorphic traits in this species seem to be absent. This contradicts the observations of Chapman (1984), who referred to an eyeless, white, troglotic species belonging to a new genus

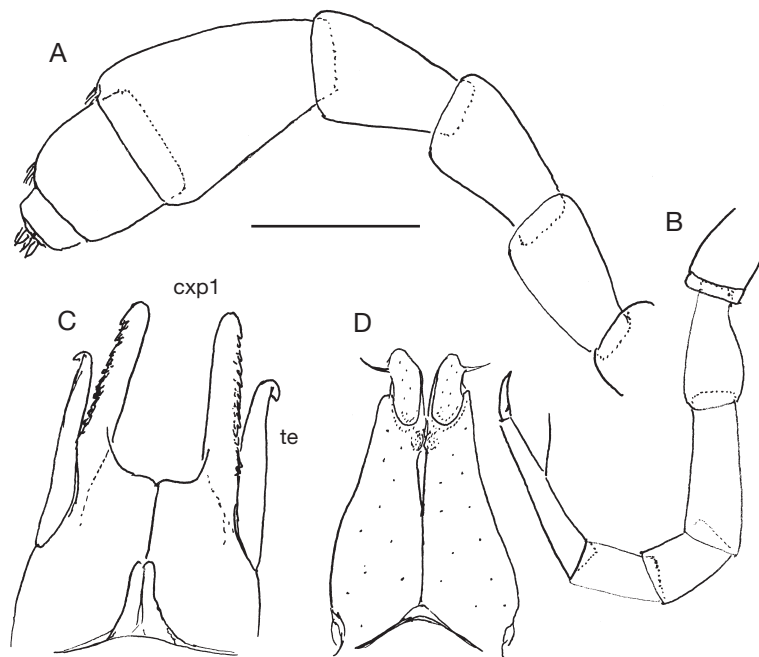


FIG. 33. — *Plusioglyphiulus hoffmani* n. sp.: paratype ♂: **A**, antenna, lateral view; **B**, midbody leg; **C**, anterior gonopods, frontal view; **D**, posterior gonopods, frontal view. Abbreviations: **cxp**, coxal process; **te**, telopodite. Scale bar: 0.3 mm.

close to *Plusioglyphiulus* as one of the inhabitants of this cave (det. R. L. Hoffman). Because the above material comes from the original sample collected by Chapman and provisionally identified by Hoffman, Chapman (1984) was certainly referring to *P. hoffmani* n. sp. The diplopod fauna of the caves of Gunung Mulu National Park is known to be rather rich and diverse, containing seven genera of four orders. Most, if not all, of

the species have been presumed to be troglobites (Chapman 1984).

Based on geographical reasons alone, when the occurrence of two congeners in the same cave is exceptional, the recent records of *P. cavernicolus* in several caves of Sarawak other than Bidi Caves, including a few caves from Gunung Mulu National Park (Decu *et al.* 2001), are most likely to represent misidentifications.

KEY TO SPECIES OF *PLUSIOGLYPHIULUS* SILVESTRI, 1923

1. At least some crests on collum complete (Figs 4A, B; 21A, B) 2
- No complete crests on collum, all interrupted (Figs 1A, B; 8A, B; 14A) 5
2. Collum with 3+3 complete crests dorsad of lateralmost crests, which are frontally abbreviated; carinotaxy pattern mixostichic. Dorsal tubercles of second row on midbody metaterga displaced, intercalary, not in line with tubercles of the other two rows. Sabah *P. macfarlanei*
- Collum with a different number of complete crests dorsad of lateralmost crests; carinotaxy pattern isostichic (i.e. devoid of intercalary tubercles or crests) (Figs 4A, B; 21A, B). Dorsal tubercles or crests arranged in clear-cut longitudinal rows (Fig. 21C, D) 3

3. Body mostly pigmented, usually brown with a pattern of yellowish markings; head between ocellaria at least partly brown. Midbody metaterga with 3/3/3+m/m+3/3/3 tubercles between poriferous cones. Male telopodites 3 stout and compact. Posterior gonopods with processes 4
 - Body completely unpigmented. Carinotaxy formula of midbody segments 3/3+1/i+2/2+m/m. Male telopodites 3 not compact, rather elongated. Posterior gonopods without processes. Cave in Sarawak *P. cavernicolus*
4. Body length 30-35 mm, width 2.0-2.2 mm. Collum with 3+3 complete crests, including lateralmost (Fig. 4A, B). Carinotaxy formula of midbody metaterga 3/3/3+1/i+3/3/3+m/m (Figs 4D; 5B). Male legs 3 strongly enlarged, typical (Figs 5D; 7D). Gonopods complex (Figs 6; 7G, H). South Vietnam *P. ampullifer* n. sp.
 - Body length about 22 mm, width 1.3 mm. Collum with 5+5 complete crests in addition to lateralmost (Fig. 21A, B). Carinotaxy formula of midbody metaterga 4/4+1/i+3/3/3+m/m (Figs 21C, D; 22A). Male legs 3 less enlarged (Fig. 23C). Gonopods simple (Fig. 23F-H). Kalimantan *P. bedosae* n. sp.
5. Carinotaxy pattern of collum isostichic (i.e. devoid of intercalary tubercles or crests). Epiproct with 1+1 high subtransverse tubercles and a median knob (Fig. 14E, F). Gonopods highly complex (Figs 16; 17F, G). Laos *P. steineri* n. sp.
 - Carinotaxy pattern of collum mixostichic. Epiproct without high subtransverse tubercles, a median knob usually missing, paramedian crests or tubercles longitudinal. Gonopods simpler 6
6. Carinotaxy formula of midbody metaterga 3/3+1/i+3/3+m/m (Fig. 1C, D). Anterior gonopods with a prominent, spiniform, median, sternal process (st) (Fig. 3C, D). Caves in Malaya *P. grandicollis*
 - Carinotaxy formulae of midbody metaterga 3/3+1/i+3/3(4)/3+m/(m)/m. Anterior gonopods without sternal process 7
7. Second transverse row of tubercles on midbody metaterga intercalary, apparently developed only towards onset of sexual maturity, formula 3/3+1/i+3/4/3+m//m. Epiproct short (Figs 27F; 32A). Legs more or less as long as body diameter. Borneo 8
 - Dorsal tubercles or crests arranged in clear-cut longitudinal rows, pattern isostichic. Epiproct longer. Legs usually closer to being half as long as body diameter 10
8. Body length 43-50 mm, width 2.0-2.1 mm; segments 64-70p+2-1a+T. Collum with a distinct transverse impression near anterior third. Carinotaxy formula of midbody segments 2/2+1/i+3/4/3+m//m (NB: Fig. 24C, D shows juvenile condition). Paraprocts flattened. Kalimantan *P. pallidior* n. sp.
 - Body length up to about 30 mm, width 1.0-1.6 mm; segments up to 53p+1a+T. Collum not particularly impressed near anterior third. Carinotaxy formula of midbody segments 3/3+1/i+3/4(5)/3+m//m. Paraprocts regularly convex 9
9. Brown spots present dorsad of ocellaria. Epiproct very short, roundly subtrapeziform (Figs 31E, F; 32A). Anterior gonopods without cxp2 (Fig. 33C). Arms (d) of posterior gonopods rudimentary (Fig. 33D). Sarawak *P. hoffmani* n. sp.
 - Brown spots absent dorsad of ocellaria. Epiproct a little longer, regularly rounded (Fig. 27E, F). Anterior gonopods swollen, stout, with both cxp1 and cxp2 (Figs 29B, C; 30G, H). Arms (d) of posterior gonopods long, spiniform and lateral in position (Figs 29D; 30I). Kalimantan *P. similis* n. sp.

10. General coloration very dark brown to blackish (fading to reddish after long conservation in alcohol). Paraprocts with a distinct, median, ridge-like elevation. Cambodia ... *P. dubius*
 — General coloration light brown to brown. Paraprocts flat medially 11
11. Paraprocts flattened (Fig. 19B). Posterior gonopods with a rather long, spiniform arm (d) (Fig. 20G) *P. deharvengi* n. sp.
 — Paraprocts regularly convex. Posterior gonopods without spiniform arm 12
12. Epiproct broadly and regularly rounded (Figs 8E, F; 9A). Posterior gonopods with rudimentary arms (d) (Fig. 10G) *P. foveatus* n. sp.
 — Epiproct roundly subtrapeziform. Posterior gonopods different 13
13. Brown spots present dorsad of ocellaria. Collum strongly impressed transversely in anterior third. Male legs 1 with very small coxites. Anterior gonopods with very short and lobe-like exp1. Posterior gonopods without arms. Cambodia *P. boutini*
 — Brown spots absent dorsad of ocellaria. Collum not particularly depressed near anterior third. Male legs 1 with large coxites (Fig. 13B). Anterior gonopods with very long, acuminate exp1 (Fig. 13F). Posterior gonopods with short, sacciform arms (d) (Fig. 13G). Thailand *P. bessoni* n. sp.

CONCLUSIONS

With the genus *Plusioglyphiulus* now comprising 14 species, it seems appropriate to provide brief analyses of the variation and distribution of its constituent species vis-à-vis the recently revised, and also basically southeast Asian, but much more speciose genus *Glyphiulus* Gervais, 1847 (Golovatch *et al.* 2007a, b). These genera are clearly closely related to one another, belonging in the same subfamily Cambalopsinae Cook, 1895. The basic differences between them lie in the more abundantly carinate/tuberculate metaterga, the special conformation of male legs 1-3, the relatively loose and complex anterior gonopods (plate-shaped in *Glyphiulus*), and the normally less compact posterior gonopods observed in *Plusioglyphiulus*.

The Cambalopsinae is generally considered to contain five genera (Mauriès 1983; Jeekel 2004): *Dolichoglyphus* Verhoeff, 1938, *Glyphiulus* Gervais, 1847, *Hypocambala* Silvestri, 1897, *Plusioglyphiulus* Silvestri, 1923 and *Podoglyphiulus* Attems, 1909. Among these, only the status of *Hypocambala* in relation to *Glyphiulus* remains to be verified in the future (see also Mauriès 1977 and his discussion of the status of *G. vietnamicus* Mauriès, 1977), based on additional collections including small juveniles of *Plusioglyphiulus*. A strange apomorphic haplopo-

dous condition of certain juvenile stadia is known from *Glyphiulus* and *Trachyiulus* genera but seems not to occur in *Hypocambala* (Enghoff 1993). The other three genera are certainly coordinate in rank with *Glyphiulus* (Golovatch *et al.* 2007a, b). *Plusioglyphiulus* is therefore treated as an independent genus, probably being the most highly evolved in the entire subfamily. This is seen from the numerous, mostly strong autapomorphies of *Plusioglyphiulus* as compared to the recently revised *Glyphiulus*.

Unlike several *Glyphiulus* species that show infra-specific variation in the division of the mentum into a pro- and eumentum, this character proves to be stable for *Plusioglyphiulus*, in which a separate promentum is always present. Similarly, variation in the degrees of setation of the gnathochilarium is very modest, that of the lamellae linguales being always oligotrichous. In other words, as in *Glyphiulus*, the structure of the gnathochilarium of *Plusioglyphiulus* species is apparently of no value at the specific level (Golovatch *et al.* 2007a, b).

As regards the carinotaxy in *Plusioglyphiulus*, the degrees of expression of crests on the collum and other body segments seem to be quite stable, in contrast to *Glyphiulus*, in which it is the patterns that are stable. Indeed, the crests and tubercles on the collum and body segments, which are always rather low (not reduced, obliterated or hypertro-

phied), barely vary in height between *Plusioglyphiulus* species. The carinotaxy patterns are relatively scarce, concerning only the midbody metaterga, and thus rather useful in classification. Even so, there are cases (*P. pallidior* n. sp. and *P. hoffmani* n. sp.) when an intercalary row of tubercles seems to appear only at or towards the onset of sexual maturity, always involving mixostichy. Thus, unlike the situation in *Glyphiulus* species, the carinotaxy formulae are only often, but not always, stable, at least so at various developmental stages. Therefore, their utility for species discrimination is not universal.

The carinotaxy patterns of the collum often vary, even intraspecifically. They always differ between species and are never correlated with those of the metaterga. The sole collar crest pattern that appears to be quite stable (though not without exceptions) can be reduced to pp/t/t+ma/t, the caudalmost row of short crests then being regular and set off by a distinct transverse sulcus from the crests or tubercles lying more anteriorly. Almost the only information that proves useful at the specific level is whether the pattern of the collum is mixo- or isostichic, and whether at least some of the crests are complete (uninterrupted). Mixostichic arrangements are prevalent. In addition, a few species, such as *P. pallidior* n. sp. and *P. boutini*, show a highly conspicuous transverse impression near the anterior third of the collum.

Variation in the carinotaxy formulae of the metaterga is more modest. The typical formulae of the midbody segments are 3/3+I/i+3/3(4)/3+m/(m)/m. Isostichy prevails. Only *P. bedosae* n. sp. shows an increased number (4/4) of crest rows below the poriferous cones, while *P. pallidior* n. sp. has a reduced number (2/2). Division of the dorsal crests into three transverse rows is a rule in *Plusioglyphiulus* species, except that *P. cavernicolus* and *P. grandicollis* have only two such rows. Similarly, among the numerous species of *Glyphiulus*, only *G. beroni* Golovatch, Geoffroy, Mauriès & Van den Spiegel, 2007 shows dorsal crests divided transversely into three rows, two rows being a rule in that genus.

Evolutionarily, it seems much easier to assume that a smooth collum and non-crested metaterga represent the plesiomorphic conditions, because most of the Juliformia, including the basalmost

ones in each of its constituent families, show poorly striated or bare tergites. This at least is the case in *Hypocambala*, which seems to be a genus particularly closely related to *Glyphiulus*. Therefore, the especially multicarinate, complex formulae, like those observed in several *Glyphiulus* and all *Plusioglyphiulus* species, can be treated as apomorphic.

Based on the similarities in gonopod structure alone, several presumably natural species groups are easily recognisable within *Plusioglyphiulus*. Thus, the *cavernicolus*-group includes *P. cavernicolus* and *P. boutini*, in which the anterior gonopods have high, characteristically curved cpx2 and short, lobuliform cpx1, while the posterior gonopods show no arm (d). Another distinct group, the *macfarlanei*-group, is represented by *P. macfarlanei* and *P. hoffmani* n. sp., in which the anterior gonopod coxites are contiguous in their basal half and supplied with just a single pair of widely separated, suberect and laterally fringed processes (cpx1), while the posterior gonopods are simple, with rudimentary arms (d) at most.

The *pallidior*-group includes *P. pallidior* n. sp. and *P. similis* n. sp., which are almost identical in gonopod structure and come from very close localities in eastern Kalimantan. Their anterior gonopods show swollen coxites and short cpx1 and cpx2, while the posterior gonopods are supplied with long, spiniform, lateral arms (d). In addition, these two species share mixostichic patterns of carinotaxy of the collum and of the midbody segments, as well as a number of other somatic characters.

Finally, the *deharvengi*-group can be distinguished to incorporate *P. deharvengi* n. sp., *P. foveatus* n. sp. and *P. bessonii* n. sp., and possibly also *P. ampullifer* n. sp., *P. steineri* n. sp. and *P. bedosae* n. sp. The anterior gonopods of these species show both cpx1 and cpx2 long and well developed, while the posterior gonopods are always supplied with arms (d).

The species *P. grandicollis* is unique in that the anterior gonopod sternite has a median process (st), and thus might also deserve a species-group of its own. As regards *P. dubius*, since its gonopod characters remain unknown, no assignment to a group is possible at present.

The general distribution of *Plusioglyphiulus* species (Fig. 34) follows a pattern of a sort of long

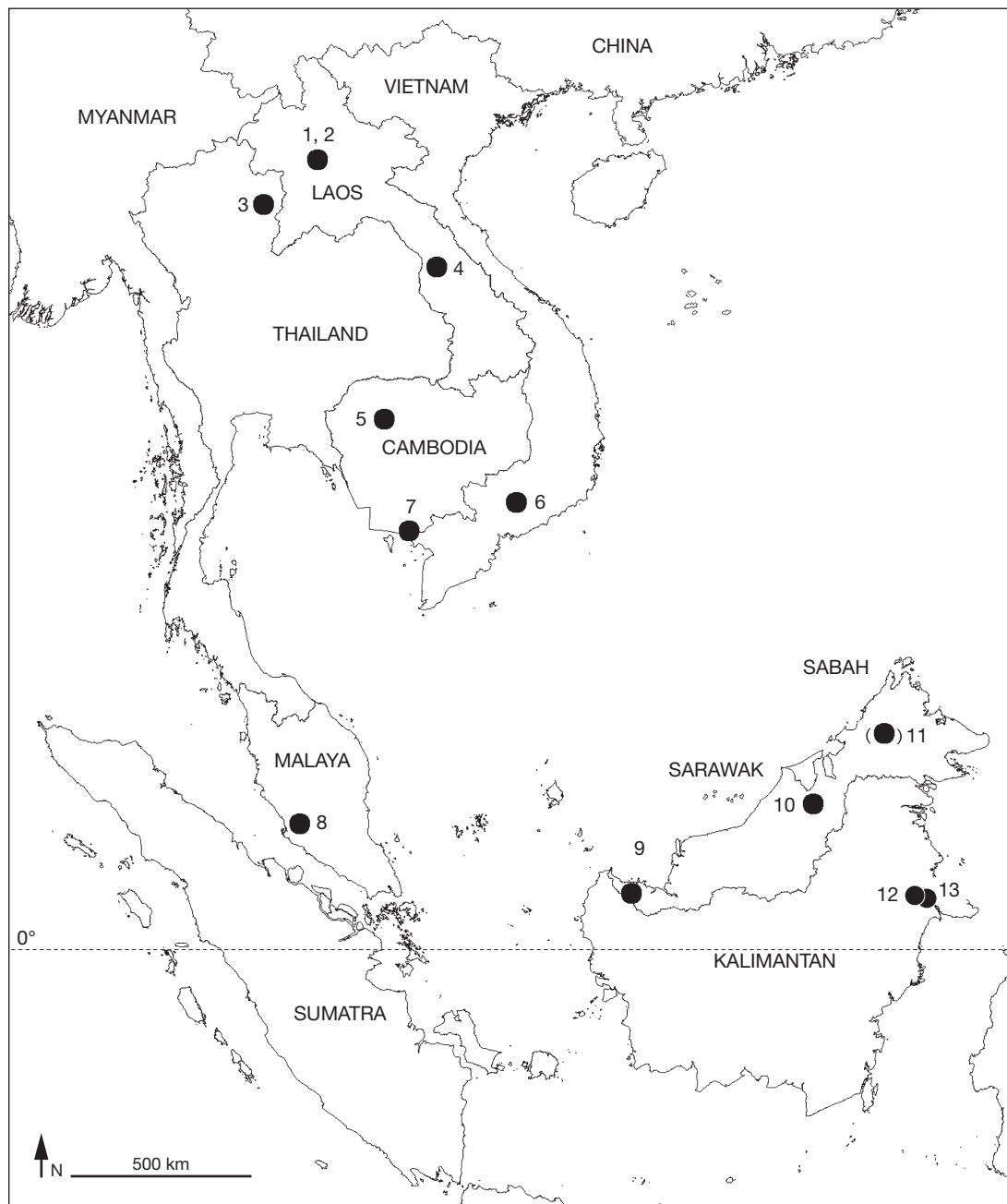


FIG. 34. — Distribution of species of *Plusioglyphiulus* Silvestri, 1923, listed more or less from northwest to southeast: 1, 2, *P. deharvengi* n. sp. and *P. foveatus* n. sp. (close but different localities); 3, *P. bessonii* n. sp.; 4, *P. steineri* n. sp.; 5, *P. dubius* Attems, 1938; 6, *P. ampullifer* n. sp.; 7, *P. boutini* Mauriès, 1970; 8, *P. grandicollis* Hoffman, 1977; 9, *P. cavernicolus* Silvestri, 1923; 10, *P. hoffmani* n. sp.; 11, *P. macfarlanei* Mauriès, 1983 (exact locality unknown); 12, *P. bedosae* n. sp. and *P. pallidior* n. sp. (same cave); 13, *P. similis* n. sp.

crescent from Indochina down through the Malay Peninsula to eastern Borneo. Probably this reflects a once continuous range around the southern end of a much lower South China Sea, the Sundaland times that can be dated back at least to the Pliocene (Hoffman 1977; Chapman 1984). Interestingly, even within such an undoubtedly homogeneous grouping like the *cavernicolus*-group, the two constituent species are greatly separated (Cambodia and western Borneo).

Several species of *Plusioglyphiulus* occur in caves but, unlike the numerous *Glyphiulus* species showing evident traits of troglomorphy, no *Plusioglyphiulus* can be unequivocally considered as true cavernicoles. They all have dark brown to blackish ocellaria (many even with an adjacent brown spot dorsally), show relatively short legs and antennae, and very few are truly pale. Significantly, whereas the evidently troglotic *Glyphiulus* species include several forms that show an ovoid body section and thin teguments, none of the *Plusioglyphiulus* species demonstrates similar conditions.

As for any reasonably large tropical genus, of which most species have only been collected from caves, above-ground explorations will certainly reveal a far richer fauna of forest-dwelling species in the region. This should be particularly true for *Plusioglyphiulus*, which does not seem to show any evident troglomorphic characters. Summarising the poor state of current knowledge, we have still only touched the tip of the iceberg (Golovatch *et al.* 2007b).

Acknowledgements

This work only became possible through the support provided to the first author by the MNHN. Yayuk Suhardjono and Cahyo Rahmadi (both MZB, Cibinong, Indonesia), Anne Bedos and Louis Deharveng (both MNHN), and Richard L. Hoffman (VMNH) are deeply thanked for the precious material they offered for study. Verena Stagl (Natural History Museum, Vienna) provided helpful information concerning some characters of the holotype of *Glyphiulus dubius* Attems, 1938 under her care. Mark Judson (MNHN) kindly corrected the English text.

Permits and field support for collecting in Kalimantan were provided by the LIPI (Indonesia) and "The Nature Conservancy" (Samarinda Branch).

REFERENCES

- ATTEMPS C. 1936. — Diplopoda of India. *Memoirs of the Indian Museum* 11: 133-323.
- ATTEMPS C. 1938. — Die von Dr C. Dawydoff in Französisch Indochina gesammelten Myriopoden. *Mémoires du Muséum national d'Histoire naturelle* N.S. 6 (2): 187-353.
- BOUTIN C. 2001. — Cambodge, in JUBERTHIE C. & DECU V. (eds), *Encyclopaedia Biospeologica*. Volume 3. Société internationale de Biospéologie, Moulis: 1755-1762.
- CHAPMAN P. 1984. — The invertebrate fauna of the caves of Gunung Mulu National Park. *Sarawak Museum Journal* 30 (51): 1-18.
- DECU V., JUBERTHIE C. & CHAPMAN P. 2001. — Malaisie (Malaysia), in JUBERTHIE C. & DECU V. (eds), *Encyclopaedia Biospeologica*. Volume 3. Société internationale de Biospéologie, Moulis: 1901-1931.
- ENGHOFF H. 1992. — The size of a millipede. *Berichte des Naturhistorisch-Medizinischen Vereins in Innsbruck, Supplementum* 10: 47-56.
- ENGHOFF H. 1993. — Haplopodous diplopods: a new type of millipede body construction discovered in cambalopsid juveniles (Diplopoda, Spirostreptida). *Acta Zoologica* 74: 257-261.
- ENGHOFF H., DOHLE W. & BLOWER J. G. 1993. — Anamorphosis in millipedes (Diplopoda) – the present state of knowledge with some developmental and phylogenetic considerations. *Zoological Journal of the Linnean Society* 109: 103-234.
- ENGHOFF H., CAODURO G., ADIS J. & MESSNER B. 1997. — A new, cavernicolous, semiaquatic species of *Serradium* (Diplopoda: Polydesmidae) and its terrestrial, sympatric congener. With notes on the genus *Serradium*. *Zoologica Scripta* 26: 279-290.
- GOLOVATCH S. I., GEOFFROY J.-J., MAURIÈS J.-P. & VAN DEN SPIEGEL D. 2007a. — Review of the millipede genus *Glyphiulus* Gervais, 1847, with descriptions of new species from Southeast Asia (Diplopoda, Spirostreptida, Cambalopsidae). Part 1: the *granulatus*-group. *Zoosystema* 29 (1): 7-49.
- GOLOVATCH S. I., GEOFFROY J.-J., MAURIÈS J.-P. & VAN DEN SPIEGEL D. 2007b. — Review of the millipede genus *Glyphiulus* Gervais, 1847, with descriptions of new species from Southeast Asia (Diplopoda, Spirostreptida, Cambalopsidae). Part 2: the *javanicus*-group. *Zoosystema* 29 (3): 417-456.
- HOFFMAN R. L. 1977. — Diplopoda from Malayan caves collected by M. Pierre Strinati. *Revue suisse de*

- Zoologie* 84 (3): 699-719.
- JEEKEE C. A. W. 1971. — Nomenclator generum et familiarum Diplopodorum. A list of the genus and family-group names in the class Diplopoda from the 10th edition of Linnaeus, 1758, to the end of 1957. *Monografieën van de Nederlandse Entomologische Vereniging* 5: i-xii, 1-412 (dated 1970, published 1971).
- JEEKEE C. A. W. 2004. — A bibliographic catalogue of the “Cambaloidea” (Diplopoda, Spirostreptida). *Myriapod Memoranda* 7: 43-109.
- KOILRAJ A. J., SHARMA V. K., MARIMUTHU G. & CHANDRASHEKARAN M. K. 2000. — Presence of circadian rhythms in the locomotor activity of a cave-dwelling millipede *Glyphiulus cavernicolus* (Cambalidae, Spirostreptida). *Chronobiology International* 17 (6): 757-765.
- MAURIÈS J.-P. 1970. — Examen des types des genres *Cambalomorpha* et *Cambalopsis* Pocock, 1895. Essai de classification des Glyphiulinae Verhoeff, 1936 (Diplopoda, Cambalidea). *Bulletin du Muséum national d'Histoire naturelle*, 2^e série, 42 (3): 509-519.
- MAURIÈS J.-P. 1977. — Le genre *Glyphiulus* Gervais, 1847, et sa place dans la classification des Cambalides, à propos de la description d'une nouvelle espèce du Viêt-Nam (Diplopoda, Iulida, Cambalidea). *Bulletin du Muséum national d'Histoire naturelle*, 3^e série, 431 (Zoologie 301): 243-250.
- MAURIÈS J.-P. 1983. — Cambalides nouveaux et peu connus d'Asie, d'Amérique et d'Océanie. I. Cambalidae et Cambalopsidae (Myriapoda, Diplopoda). *Bulletin du Muséum national d'Histoire naturelle*, 4^e série, section A, 5 (1): 247-276.
- SILVESTRI F. 1923. — Descriptions of some Indian and Malayan Myriapoda Cambaloidea. *Records of the Indian Museum* 25 (2): 181-193.

*Submitted on 29 November 2006;
accepted on 11 April 2008.*